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AN INDIVIDUAL-BASED APPROACH TO THE FORAGING BEHAVIOR AND ENERGETICS OF A GENERALIST MARINE PREDATOR

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ABSTRACT

An individual-based approach to the foraging behavior and energetics of a generalist marine predator

by

Elizabeth Alexis McHuron

Foraging behavior is a key ecological factor that has wide-ranging implications for individual fitness, and population and ecosystem dynamics. There are multiple hierarchical levels at which foraging behavior can be studied, from broad descriptions at the species level to the lowest level of within-individual variability. Intraspecific variation in foraging behavior is increasingly recognized as both widespread and ecologically important, and the occurrence and consistency of individual variation in foraging behavior has implications for the ability of populations to adapt to environmental change. The focus of my dissertation is on quantifying inter- and intra-individual variability in foraging behavior and the energetic implications of these differences for California sea lions (*Zalophus californianus*), an abundant generalist predator that inhabits a dynamic ecosystem. The fine- and broad-scale foraging behavior of adult female sea lions was quantified at multiple temporal scales using bio-logging technology and stable isotope analysis. Concurrent measurements of foraging behavior and energy expenditure were used to determine the energetic implications of behavioral variability. I found that female California sea lions used three foraging strategies: a shallow epipelagic strategy, a mixed epipelagic/benthic strategy, and a deep-diving strategy. This diversity in foraging behavior has likely allowed them to be successful in such a dynamic ecosystem, as I found evidence that female sea lions switched foraging strategies in response to changes prey availability. Despite this apparent flexibility, females generally exhibited behavioral consistency across both short and long time scales, including periods of reduced prey availability. Collectively, these results indicate that female California sea lions likely do switch foraging strategies, but it is unlikely that most sea lions routinely use all three strategies. Instead, they largely appear to play it safe by consistently using similar habitats and/or dive behaviors, which may be a successful strategy for managing uncertainty in environmental conditions. These individual behavioral differences have implications for survival and fitness, as fine-scale behavior affected the rate of energy expenditure. My dissertation highlights the importance of quantifying inter- and intra-individual variation in foraging behavior, particularly as it relates to understanding the strategies that individuals and species use to cope with limited prey resources in dynamic environments.

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INTRODUCTION

Foraging behavior is a critical component influencing the survival and reproductive fitness of individuals. Because the end result of foraging is energy acquisition, foraging behavior influences not only population dynamics, but also can affect community and ecosystem structure through species interactions and trophic cascades (Estes and Duggins 1995; Carpenter et al 2001; Terborgh et al 2001; Ripple and Beschta 2004; Croll et al 2005). There are multiple hierarchical levels at which foraging behavior can be studied, from broad descriptions at the species level to the lowest level of within-individual variability. Intraspecific variability in foraging behavior was traditionally considered ‘noise’ in ecological studies, with species often classified into broader groups based on their use of available resources (‘generalists’ or ‘specialists’). This view has largely changed in the last several decades, as it is increasingly recognized that individual variation is both widespread and ecologically important, even for seemingly generalist species (Bolnick et al 2003; Araújo et al 2011; Tinker et al 2012; Cantor et al 2013; Ceia and Ramos 2015; Rosenblatt et al 2015; Kernaléguen et al 2016).

Marine mammals are a diverse group of aquatic and semi-aquatic species that are important components of marine ecosystems worldwide, mainly as a result of their abundance, large body size, and relatively high trophic level (Bowen 1997; Morissette et al 2006; Kiszka et al 2015). The foraging behavior of marine mammals is challenging to study given their aquatic and often elusive nature, but the development of bio-logging technology and biochemical techniques have revolutionized our understanding of what, how, and where foraging occurs (Kooyman 2004; Rutz and Hays 2009). The use of bio-logging devices typically results in fine-scale behavioral data for a small number of individuals, allowing for the examination of inter- and intra-individual variation in foraging behavior across a variety of temporal scales. This approach has revealed that many marine mammal species use multiple foraging strategies, and that behavioral differences are prevalent even among individuals within 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). Foraging strategies often reflect the three basic diving patterns exhibited by marine predators (epipelagic, mesopelagic, benthic), but also may be related to habitat use, oceanographic features, temporal differences, and site fidelity. Despite the dynamic nature of marine environments, individual variation in dive behavior, movement metrics, and diet in marine mammals is often consistent through time (Estes et al 2003; Bradshaw et al 2004; Chilvers 2008; Arthur et al 2015; Ceia and Ramos 2015; Orben et al 2015; Rossman et al 2015; Wakefield et al 2015).

The focus of my dissertation is on quantifying inter- and intra-individual variability in foraging behavior and the energetic implications of these differences for California sea lions (*Zalophus californianus*), a generalist marine predator found along the West Coast of the United States. I focused on adult female California sea lions as they are central-place foragers during the 10 - 11 month lactation period, alternating foraging trips to sea with time onshore nursing a single pup (Melin et al

2000; Melin et al 2008; Kuhn and Costa 2014). The foraging behavior and energetics of female sea lions during this time is particularly important as their success (or lack thereof) has direct implications for the growth and survival of their dependent pup. In Chapter 1, I describe the different foraging strategies that female sea lions use, and discuss the energetic and reproductive implications of these strategies. In Chapter 2, I quantify the energy expenditure of female sea lions, and examine how fine- and broad-scale behavioral differences affect energy expenditure. In Chapter 3, I describe the growth dynamics of California sea lion whiskers and explore several methods for quantifying whisker growth rates of free-ranging California sea lions. Chapter 3 is relevant because biochemical analysis of whiskers is frequently used to examine individual variation in foraging behavior, but interpretation of these data in an ecological context requires knowledge of the duration and rate of growth. This method is applied in Chapter 4 to quantify intra- and inter-individual variability in broad-scale foraging behavior across multiple years. In Chapter 4, I quantify how consistent individual sea lions are in their fine- and broad-scale foraging behaviors, and examine the factors that contribute to individual differences in behavioral consistency. Collectively, my dissertation provides an in-depth investigation into the foraging behavior and energetics of adult female California sea lions, which is critical for understanding population responses of this abundant predator to environmental changes.

CHAPTER 1

Flexibility is key: short-term individual specialization in a successful marine predator

McHuron, E.A., Robinson, P.W., Simmons, S.E., Kuhn, C.E., Fowler, M., and D.P. Costa

1.1. Abstract

Intraspecific competition may drive the diversification of foraging behavior in resource-limited environments, which has broad implications for population and community ecology. We used bio-logging data and stable isotopes to examine individual differences in foraging behavior of California sea lions (*Zalophus californianus*), a successful top predator inhabiting the dynamic California Current Ecosystem. Adult female California sea lions ($n = 35$) used one of three strategies on foraging trips to sea: a shallow, epipelagic strategy, a mixed epipelagic/benthic strategy, and a deep-diving strategy. Differences in dive behavior and δ^{15}N values suggest at least some degree of dietary specialization among strategies. Sea lions were flexible in their foraging behavior, with individual sea lions using between one and all three foraging strategies across multiple trips to sea. There also was inter-annual variation in the prevalence of each foraging strategy, indicating that California sea lions do not exhibit long-term fidelity to a single foraging strategy. Sea lions using the shallow and mixed benthic strategies travelled farther and had longer trip durations than sea lions using the deep-diving strategy, yet did not spend any additional time hauled-out at the rookery. The apparent lack of long-term specialization and the importance of all three diving patterns (epipelagic, benthic, and mesopelagic) are relatively unique among otariid carnivores (fur seals and sea lions).

This flexibility has likely been a key to the continued success of California sea lions in an environment where prey availability fluctuates both seasonally and annually.

1.2. Introduction

Intraspecific variability in foraging behavior can occur within populations as a mechanism to reduce competition, both within and among demographic groups. Individuals under resource-limited conditions are often more specialized in their behavior than individuals with access to abundant resources (Svanbäck and Bolnick 2007; Tinker et al 2008), although the effect of intraspecific competition on specialization appears to be context dependent (Elliott Smith et al 2015; Newsome et al 2015). Individual specialization, whereby individuals use only a subset of the available resources, has been documented in a diverse range of taxa, but appears to be particularly common in upper trophic level consumers (Bolnick et al 2003; Araújo et al 2011). The presence of specialization within populations affects individual fitness and can be important in structuring population and community dynamics (Johnson et al 2009; Schreiber et al 2011; Bolnick et al 2011).

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 association 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), with an estimated population size of 297,000 individuals (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), but there is evidence that this generalist pattern may not extend to the individual level (Weise et al 2010; Villegas-Amtmann et al 2011). Mechanisms that reduce intraspecific competition may be particularly important for lactating females because they have a limited distribution during an energetically expensive time period (Williams et al 2007). During the 10-11 month lactation period, females are based at one of many breeding rookeries in southern California, alternating foraging trips to sea (1 - 7+ days) with onshore nursing (1 - 2 days) at the rookery (Melin et al 2000; Kuhn and Costa 2014). Females are therefore restricted to foraging in southern and central California waters, which likely leads to high intra- and inter-rookery competition, especially during periods of reduced food availability.

Despite their abundance and role as an indicator of ecosystem conditions in the CCS (Melin et al 2012), 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 U.S. rookeries (San Miguel and San Nicolas Islands) exhibited considerable individual variation in their at-sea behavior. An individual-based approach is necessary to better understand the strategies that females may use to reduce intraspecific competition, and how females respond to the seasonal, annual, and multi-year changes in prey availability that are characteristic 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 (Wells et al 2013; Leising et al 2014).

We used data from bio-logging devices to determine if adult female California sea lions exhibit multiple foraging strategies. The specific objectives were to (1) identify and describe foraging strategies of female sea lions, (2) determine whether the prevalence of each strategy varied among years, (3) identify potential dietary differences among strategies using stable isotopes, (4) examine spatial use of each foraging strategy, and (5) determine if movement and haul-out behaviors differed among strategies. An understanding of individual foraging strategies can help elucidate the potential trade-offs sea lions face in terms of physiological constraints, pup attendance, and energy expenditure that may impact overall fitness.

1.3. Methods

Data collection

Lactating adult female California sea lions (*n* = 41) were captured in November of 2005 to 2008 at San Nicolas Island (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 and blood samples were collected at the time of initial capture. Blood samples were stored on ice in the field and later centrifuged; plasma samples were removed and stored in plastic cryovials at -20 °C. Sea lions were recaptured approximately two months later to recover instruments and obtain the complete, archived dive record.

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 travelled from the rookery (km), total distance travelled (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 travelled 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 females 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 travelled from the rookery and 7.1 ± 41.5 km for total distance travelled).

Dive data were analyzed using a custom built zero-offset correction and analysis program in MATLAB (IKNOS, Y. Tremblay). Only dives deeper than 4m 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 5 dives with a maximum surface interval of 10 minutes 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; Villegas-Amtmann 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. The diel index was calculated as the difference between the mean maximum day and night dive depths divided by the greater of the two depth values. 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 hr^{-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 sea floor), mesopelagic (≥ 200 m), and deep benthic (≥ 200 m and at or near the sea floor). 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 (~5,000 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 each sea lion. All presumed benthic dives (shallow and deep) were subsequently combined into one dive type.

Stable isotope analysis

Plasma samples collected at the initial capture were analyzed for carbon (C) and nitrogen (N) stable isotopes. These two isotopes can be used as indicators of habitat use (C) and trophic position (N), and are often used as proxies for diet (Newsome et al. 2010). Samples were freeze-dried for 48 hours, homogenized, and weighed into tin capsules (0.5 ± 0.05 mg). They were analyzed using a Carlo-Erba NE2500 CHNS-O Analyzer coupled to a Thermo Finnigan DELTAplus XP Isotope Ratio Mass Spectrometer via a Thermo Finnigan ConFlo III at the University of

California Santa Cruz Stable Isotope Laboratory. Results are expressed as a ratio using delta (δ) notation in units of parts per thousand (‰). Values were calculated from the equation $\delta X = [R_{sample} / R_{standard}) - 1] \times 1000$ where X = ^{15}N or ^{13}C and R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$ in the sample and standard. The standard for C was Vienna-Pee Belemnite Limestone, and atmospheric N_2 (air) for N. Replicates of an internal laboratory standard were used to assess precision; mean differences were 0.07 ‰ for $\delta^{13}C$ and 0.1 ‰ for $\delta^{15}N$.

Statistical analysis

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 (McGarigal et al 2002). 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

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

where $\bar{x}_q$ is the mean of a dive variable for group q and $\bar{x}$ 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.

Differences in δ^{13}C and δ^{15}N values among foraging strategies were assessed using ANOVAs. For δ^{15}N values, we used an ANOVA with a Welch's correction because of unequal variances among foraging strategies. Year was not included in the analysis due to small sample sizes for each strategy/year combination, but no strategy was represented by samples collected from just one year. Post-hoc comparisons for δ^{15}N were made using a Dunnett-Tukey-Kramer test, which adjusts for unequal variances and sample sizes. Because the half-life of isotopes in plasma is ~ 7 days (Hilderbrand et al 1996), plasma samples should represent the foraging behavior of a female over one or two trips to sea. The foraging strategy of each female over the time period represented by the plasma samples was unknown because the blood sample was collected at the time of instrumentation. We therefore assigned a foraging strategy to each sample based on the strategy of the first trip to sea following instrumentation. Samples were only included if, at minimum, the first two trips were classified to the same foraging strategy. This approach was used because visual examination of the data indicated that even when females used more than one foraging strategy across the tracking period, successive trips tended to be in the same foraging strategy (i.e., strategies were clumped in time).

The horizontal spatial use of each foraging strategy was described using a kernel density analysis of the location of dive bouts (Geospatial Modelling 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-effects 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 travelled from the rookery, total distance travelled, 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 therefore 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 $p \leq 0.05$.

1.4. 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). The mean tracking duration per year ranged from 53 - 77 days, with an overall mean of 60 ± 16 days. The number of trips per individual ranged from 3 - 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 (84.2 ± 9.3 kg) and 150 to 173 cm (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 1.1). The cluster analysis identified three distinct foraging strategies that were largely discriminated on the first two principal component dimensions (Figure 1.1). 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 epipelagic/mesopelagic strategy (Strategy 3; Figure 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 1.2). 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 1.2). 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 1.2). In general, the mass range of females was similar across all three strategies; however, 93% of females with foraging trips in Strategy 3 were over 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 one strategy), and the remaining 34% using two or all three strategies. All strategies were represented in every year, but the prevalence of Strategy 1 ($F_{3,31} = 3.24$, $p = 0.04$) and Strategy 2 ($F_{3,31} = 4.26$, $p = 0.01$) varied among years. For Strategy 1, the mean prevalence (± SE) was significantly higher in 2005 (average of 69 ± 13% of a female's trips were in this strategy) compared with 2008 (15 ± 10%, $p_{2005\text{-}2008} = 0.03$), but neither year was different from 2006 (39 ± 18%, $p_{2005\text{-}2006} = 0.20$, $p_{2006\text{-}2008} = 0.72$) or 2007 (35 ± 13%, $p_{2005\text{-}2007} = 0.21$, $p_{2006\text{-}2007} = 0.99$). Strategy 2 was uncommon in 2005, with a mean prevalence of 12 ± 17 %, which was significantly lower than 2008 (61 ± 14 %) and marginally non-significant from 2006 (44 ± 14%, $p = 0.08$). The prevalence of Strategy 3 ranged from 17% to 45%, but there was no significant difference among years ($F_{3,31} = 1.07$, $p = 0.38$).

A total of 19 plasma samples were collected from females between 2006 and 2008 that could be confidently assigned to a foraging strategy. The isotope values of these females ranged from -18.1 to -16.0 ‰ for δ^{13}C and 16.1 to 17.4 ‰ for δ^{15}N. The mean δ^{13}C values (± SE) for each strategy were -17.1 ± 0.2 ‰ (Strategy 1, n = 8), -16.8 ± 0.2 ‰ (Strategy 2, n = 7), and -17.3 ± 0.2 ‰ (Strategy 3, n = 4). The mean δ^{15}N values (± SE) for each strategy were 16.5 ± 0.2 ‰ (Strategy 1), 17.0 ± 0.1 ‰ (Strategy 2), and 17.4 ± 0.02 ‰ (Strategy 3). There were differences in δ^{15}N values ($F_{2,8.8} = 19.95$, $p < 0.001$) but not δ^{13}C values ($F_{2,16} = 0.93$, $p = 0.42$) among strategies. Females in Strategy 3 had significantly greater δ^{15}N values than females in the other two strategies (Strategy 1: $p < 0.01$, Strategy 2: $p = 0.03$), but there was no significant difference between δ^{15}N values of females in Strategies 1 and 2.

Spatial use and movement/haul-out behavior

Core foraging areas were variable among strategies and years (Figure 1.2d-f, Figure 1.3). 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 travelled ($F_{2,23.8}$ = 14.80, $p < 0.01$) with strategy. Foraging trips in Strategy 3 were significantly shorter in duration, closer to the rookery, and had less total distance travelled than the other two strategies (Table 1.3). 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 1.3). 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 2 were more likely to haul-out on foraging trips compared with females using Strategy 3 (Table 1.3). 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 1.3).

1.5. Discussion

The presence of multiple foraging strategies for adult female California sea lions indicates that specialization exists within this demographic group, and females are more than simply shallow, epipelagic foragers. 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; Villegas-Amtmann et al 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; Villegas-Amtmann et al 2011). This flexibility in diving strategies, coupled with a strong dependence on epipelagic foraging, may have contributed to the recovery of California sea lions post-exploitation. This is in contrast to many of the other primarily-benthic foraging sea lion species that have not recovered from exploitation and/or are experiencing population declines (Costa et al 2004; Arnould and Costa 2006).

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 opolescens*; (Lowry et al 1988; Lowry and Carretta 1999; Orr et al 2011). Differences in diving behavior, spatial use, and isotope values among strategies indicate at least some degree of diet specialization across the three foraging strategies. The importance of specific prey species in the diet fluctuates annually (Lowry et al 1988; Orr et al 2011; Melin et al 2012), which is likely why we found differences in the prevalence of each strategy among years. There are no diet data available for California sea lions at any of the southern California rookeries for the time period (year and season) that adult females were tagged, but there is limited evidence that the diets of female sea lions at different rookeries may partially overlap (Lowry and Carretta 1999). 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). In 2006, sardine and anchovy were both important, but juvenile hake and juvenile and adult market squid also occurred frequently in scat samples (Orr et al 2011). The shallow, epipelagic strategy (Strategy 1) was common in 2005, which may indicate that sea lions using this strategy primarily targeted small, schooling fishes. Hake and market squid may have been the target prey of females using the mixed epipelagic/benthic strategy (Strategy 2) because the increased prevalence of this strategy in 2006 coincided with the increased frequency of occurrence of these species in scat samples at San Miguel Island. 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 to 3 km of the northern Channel Islands and mainland coast from November to April (Zeidberg et al 2012). Females in Strategy 2 had slightly greater δ^{15}N values than females in Strategy 1, but these differences were not significant. This may have been because of overlap in δ^{15}N values among prey species (Becker et al 2007; Madigan et al 2012; Miller et al 2013) or because of overlap in the diet of females in these strategies.

Deep-diving sea lions (Strategy 3) had greater δ^{15}N values than sea lions in the other two strategies, suggesting they targeted at least one species not consumed by females in the other two strategies. Mesopelagic fishes, such as California lanternfish (*Symbolophorus californiensis*), northern lampfish (*Stenobrachius leucopsarus*), and California smoothtongue (*Leroglossus stilbius*), are found in scats of sea lions from both San Miguel and San Nicolas Islands (Lowry et al 1988; Orr et al 2011; Melin et al 2012). Miller et al (2013) found mean δ^{15}N values of 14.4 ‰ (California lanternfish and northern lampfish) and 14.8 ‰ (California smoothtongue) in fish collected from the northern California Current, which were higher than values for northern anchovy (13.8 ‰), sardine (12.6 ‰), hake (12.7 ‰), and market squid (12.8 ‰). Hake, market squid, and other cephalopod species found in sea lion scat can be associated with the shelf break and continental slope (Mackas et al 1997; Hunt and Seibel 2000), and are therefore also potential prey items for sea lions using Strategy 3. There was considerable variation in dive depth, percentage of mesopelagic dives, and diel behavior among sea lions using Strategy 3, which may indicate further specialization within this strategy.

California sea lions only exhibited short-term fidelity to a given foraging strategy, with some individuals using more than one strategy during the study period. In addition, differences in the prevalence of each strategy among years support the conclusion that females may not exhibit interannual fidelity to one strategy. This behavior is in contrast to the long-term individual specialization exhibited by many other species (Estes et al 2003; Woo et al 2008; Thiemann et al 2011; Kernaléguen et al 2012; Robertson et al 2014). 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, productive season. Short-term specialization may therefore be a more general characteristic of this species. The apparent lack of long-term individual specialization may be because it does not increase search or capture efficiency, which has been suggested as a potential factor driving dietary specialization for other species (Dall and Cuthill 1997; Bernays and Funk 1999; Tinker et al 2009), or because the dynamic nature of the CCS makes long-term specialization unprofitable.

Despite the flexibility of individual female California sea lions to use multiple foraging strategies, 40% of the sea lions in our study used only one strategy. Variability in fidelity did not appear to be linked to one particular strategy, as there were sea lions that specialized in each of the three foraging strategies. Differences in behavioral consistency may have been driven by prey availability, although in each of the four years there were always some sea lions that used only one strategy and others that used a variety of strategies. Alternatively, this variability may be an indication that individual California sea lions may adopt either a generalist or specialist foraging strategy, with some individuals exhibiting greater consistency in either diet or dive behavior than others. The presence of both dietary specialists and generalists within populations appears quite common for both marine and terrestrial species (Araújo et al 2010; Tinker et al 2012; Cantor et al 2013; Kernaléguen et al 2016). For California sea lions, the apparent presence of short-term specialists and generalists could be related to individual differences in foraging success (e.g., as a result of age or experience), or reflect morphological, physiological or behavioral differences (i.e., personality; (van Oers et al 2004; Bergvall et al 2011; Patrick and Weimerskirch 2014) among individuals.

Individuals may be excluded from some foraging strategies due to physiological constraints, which might have played a role in the ability of female sea lions in our study to use all three strategies. The diving ability of marine mammals is constrained by their available onboard oxygen stores and the rate at which they use those stores (Kooyman and Ponganis 1998). Diving capabilities typically increase with mass due to increased total body oxygen stores coupled with lower mass-specific metabolic rates. Several studies have found differences in the mass or body size of sea lions in different foraging strategies, with smaller individuals constrained to shallow-diving strategies (Villegas-Amtmann et al 2008; Weise et al 2010); however, other studies have detected no such relationships (Chilvers and Wilkinson 2009; Baylis et al 2015). In our study, the mass range of females was similar among all three foraging strategies (62 - 97 kg), but the mass of all but one of the animals that used the deep-diving strategy (Strategy 3) was greater than 79 kg. This may indicate that in general females less than 80 kg do not have the physiological capabilities to successfully use this strategy.

Foraging strategies are often spatially explicit and individuals using different strategies may therefore have to travel varying distances to foraging areas (Chilvers and Wilkinson 2009; Arnould et al 2011; Lowther et al 2011; Kernaléguen et al 2012; Baylis et al 2015). We found some overlap in the core foraging areas of sea lions using different strategies, but there were differences in movement and haul-out variables among foraging strategies. Female sea lions using Strategies 1 and 2 travelled farther and had longer trip durations than sea lions using Strategy 3. Longer trip durations were primarily the result of greater travel distances, 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 may have affected pup condition because pups of females using Strategies 1 and 2 fasted for longer, yet there were no significant differences in the amount of time spent at the rookery among strategies. For example, in one month an average female sea lion using Strategy 3 would spend 24% more time at the rookery than a female using Strategy 1 (7.7 days vs. 6.2 days). Although they did not increase the duration of onshore visits, sea lions using Strategies 1 and 2 may have compensated for longer trip durations by increasing the time spent suckling the pup while onshore. Ultimately, the ability of females to mitigate the effects of trip duration on pup condition likely depends on the energetic expenditure and prey quality associated with each foraging strategy.

Energetic expenditure likely varied among foraging strategies due to differences in both diving and movement behavior. Benthic diving is often assumed to be an energetically expensive strategy (Costa et al 2004); however, other factors such as such as the proportion of time at sea spent diving, dive depth, and travel distances may also affect energy use (Arnould et al 1996; Costa and Gales 2000; Costa and Gales 2003). For example, the energy use 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 travelling between prey patches (Arnould et al 1996). In our study, sea lions using Strategy 2 spent the greatest proportion of time at sea diving (39%) and had the greatest proportion of benthic dives, whereas sea lions using Strategy 3 had the lowest proportion of time at sea spent diving (23%), greatest dive depths, and lowest dive rates. The low dive rate and proportion of time at sea spent diving for sea lions using Strategy 3 was likely due to an increased amount of time on the surface resting and not time spent travelling between patches, as these females used a very restricted foraging area. We would therefore hypothesize that females using Strategy 2 may have had the highest energy expenditure, especially considering that these sea lions travelled farther than those in 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). The prey of California sea lions varies dramatically in lipid content, but schooling fishes have higher lipid content than hake, market squid, and rockfish (Huynh and Kitts 2009; Litz et al 2010). This may indicate that high cost might not result in a high reward for California sea lions, which has also been suggested for foraging strategies of New

Zealand sea lions (Chilvers and Wilkinson 2009) and northern fur seals (Costa and Gentry 1986); however, the ultimate success of a strategy is dependent not only on the energy content but the availability of prey. Thus, sea lions that use a high cost, low reward strategy may still be successful in years of abundant resources.

Conclusion

Adult female California sea lion have both the ability to employ a range of diving strategies and the flexibility to switch strategies. This is relatively unique among otariids and has likely been a key to the continued success of this species in an environment where prey availability fluctuates both seasonally and annually. Intraspecific competition is one of the many factors that may drive individual specialization within populations (Tinker et al 2008; Matich et al 2011; Kernaléguen et al 2015; Robertson et al 2015), and we hypothesize that the presence of multiple foraging strategies for female California sea lions at San Nicolas Island is at least in part driven by limited prey resources. This individual variation should be recognized when interpreting and predicting population-level responses of California sea lions to oceanographic variability, especially considering the potential energetic and reproductive tradeoffs among 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. Results from this study contribute to a growing body of literature that highlights the importance of accounting for individual specialization 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.

1.6. Acknowledgements

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Table 1.1. 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 hr^{-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)

Table 1.2. Mean (± 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 hr^{-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 0-1, 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)

Table 1.3. 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 $p \leq 0.05$

[**] Represent 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

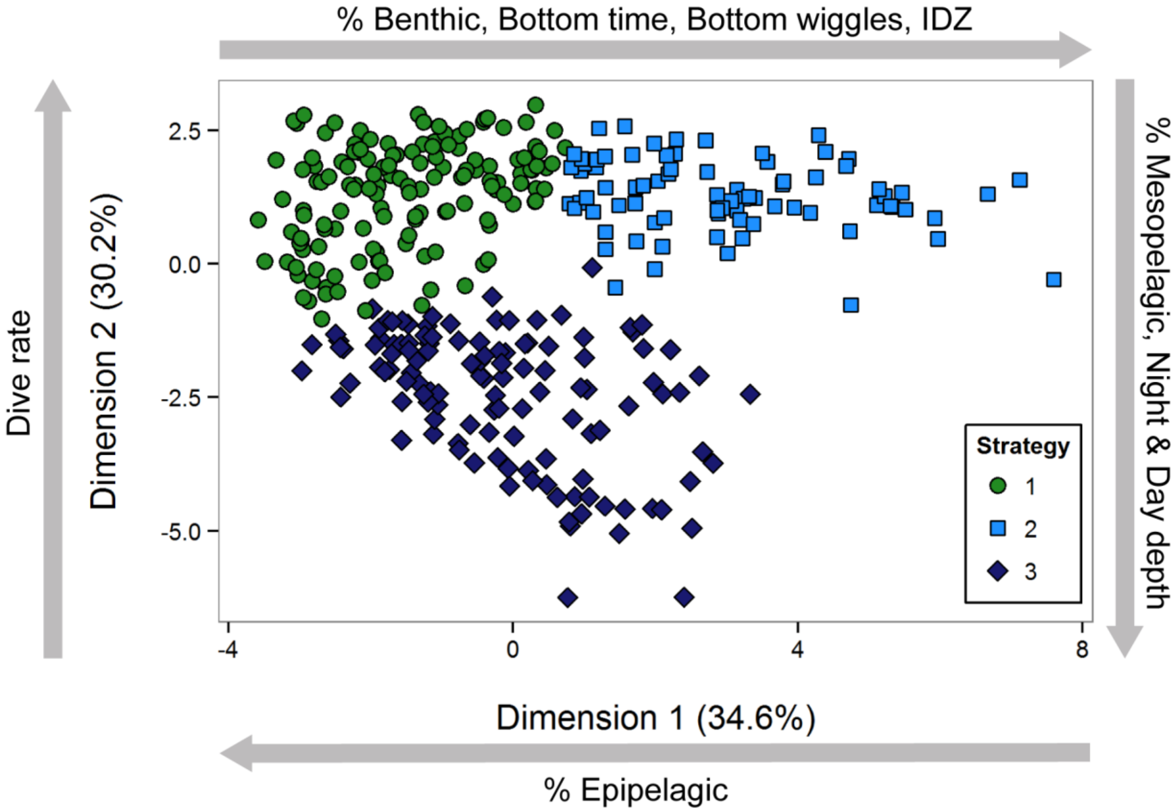

Figure 1.1. The three foraging strategies exhibited by adult female California sea lions from San Nicolas Island as identified by a hierarchical cluster analysis of principle components. The location of each point, corresponding to one foraging trip and color-coded by strategy, is shown on the first two principal component dimensions. The dive variables that loaded strongly (> 0.7) on each dimension are above arrows indicating the direction of each relationship.

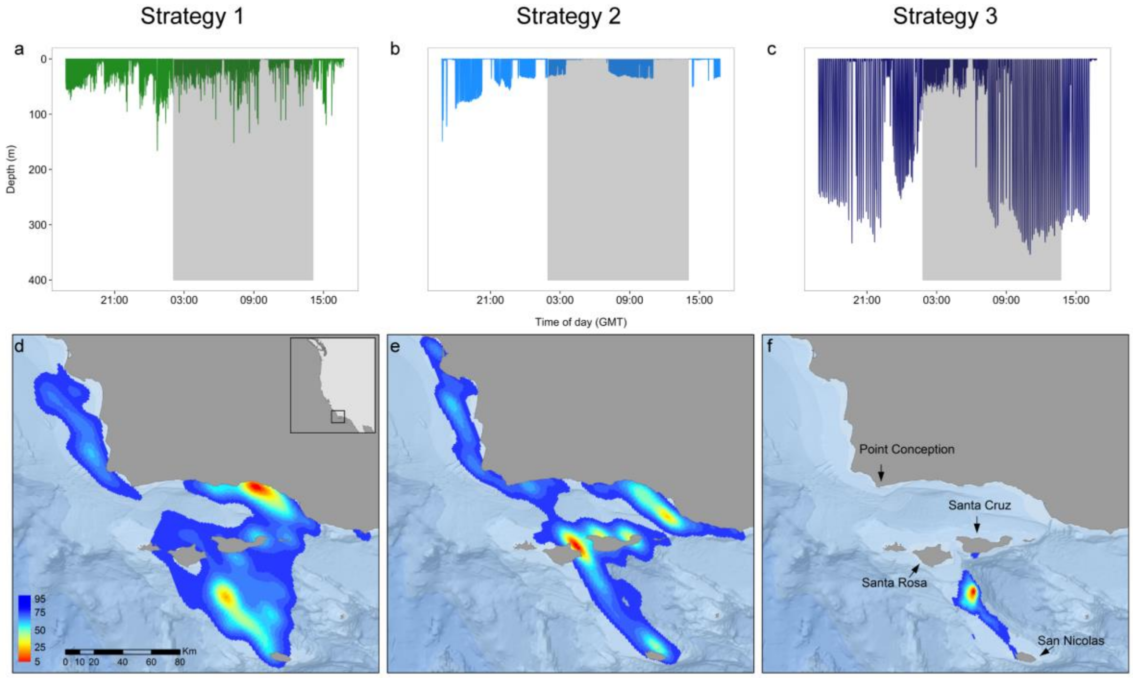

Figure 1.2. Dive profiles for representative 24-hour periods (a - c) and kernel density analysis of all dive bout locations between 2005 and 2008 showing 95% utilization distributions (d - f) for each of the three foraging strategies exhibited by adult female California sea lions from San Nicolas Island. Strategy 1 is a shallow, epipelagic strategy, Strategy 2 is a mixed epipelagic/benthic strategy, and Strategy 3 is a deep epipelagic/mesopelagic strategy. In the top panel, the gray boxes represent local night. In the bottom panel, warmer colors indicate higher use and cooler colors represent lower use.

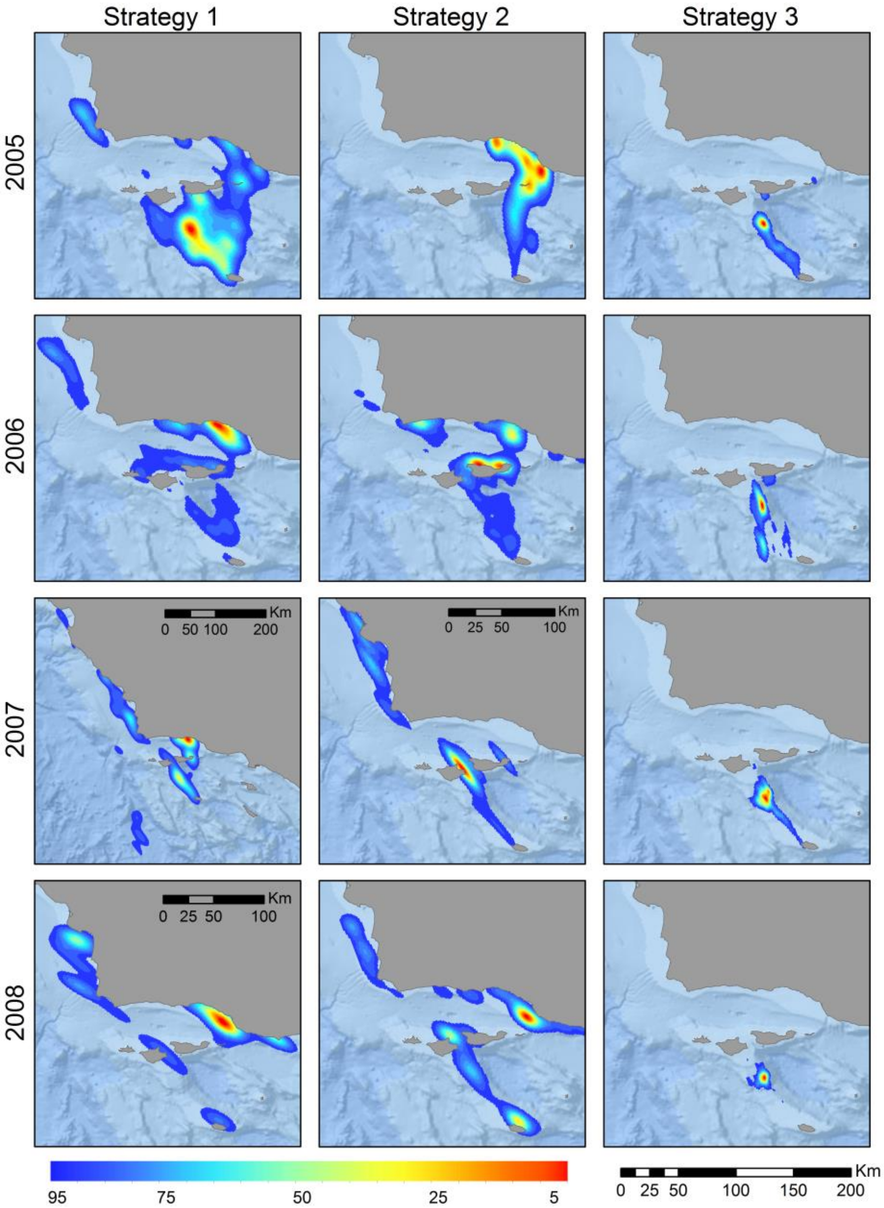

Figure 1.3. Kernel density analysis of dive bout locations showing 95% utilization distributions per year for the three foraging strategies exhibited by adult female California sea lions from San Nicolas Island. Strategy 1 is a shallow, epipelagic strategy, Strategy 2 is a mixed epipelagic/benthic strategy, and Strategy 3 is a deep epipelagic/mesopelagic strategy. In all plots, warmer colors indicate higher use and cooler colors represent lower use. San Nicolas Island is located in the lower right hand corner. Separate scale bars are provided for subplots that differ in scale.

CHAPTER 2

Behavioral drivers of energy expenditure in a flexible marine predator

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2.1. Abstract

Energy expenditure is a key physiological measurement with broad ecological and conservation applications. Intraspecific variability in energy expenditure is affected by animal behavior, either through changes in time-energy budgets or individual variation in foraging behavior. The relationship between energy expenditure and behavior is not well understood for large carnivores, yet is crucial for understanding how natural and anthropogenic factors may influence individual fitness and population dynamics. We measured at-sea field metabolic rates (at-sea FMR) in conjunction with dive and movement behavior of lactating female California sea lions (*n* = 16), a large marine carnivore that exhibits considerable behavioral flexibility. There was considerable individual variability in at-sea FMRs, which ranged from 3.29 to 6.97 W kg^{-1}. The behavior of sea lions could be classified into one of two general foraging strategies, although there was also behavioral variability within each foraging strategy. The mean energy expenditure of sea lions was generally higher than previous estimates for this species, which may have been due in part to changes in time-energy budgets as a result of poor prey availability during our study. At-sea FMRs of benthic-diving sea lions increased with dive depth and duration, but this relationship did not hold for deep-diving sea lions. Sea lions undertaking long and/or deep benthic dives spent more time at the bottom of the dive, indicating that energy

expenditure likely increases as sea lions spend more time actively swimming in the search and pursuit of prey. Our results suggest that while fine-scale behavioral differences can impact energy expenditure, these relationships differ among foraging strategies. As a result, there may not be a common set of variables that explain intraspecific variability in energy expenditure for marine carnivores that use multiple foraging strategies or dive types.

2.2. Introduction

The tradeoff between energy expenditure and acquisition is a key factor influencing the survival and reproductive fitness of organisms. Energy expenditure encompasses costs associated with maintenance demands, thermoregulation, feeding, locomotion, and growth; collectively, these costs are referred to as an animal's field metabolic rate (FMR). There are a variety of intrinsic and extrinsic factors that impact FMR and drive inter- and intraspecific variability in energy expenditure. Body size is perhaps the most ubiquitous and influential factor, although other factors, such as phylogeny, trophic group, temperature, and animal behavior can also affect energy expenditure (Anderson and Jetz 2005; Nagy 2005). Behavior influences FMR because some activities inherently differ in their energetic cost (e.g., foraging, resting); consequently, the amount of time spent in each activity (time-energy budget) affects FMR. For similar reasons, foraging behavior is also important in driving inter- and intraspecific variability in FMR, as animals may use different tactics to find and capture prey that vary in their energetic costs (Nagy et al 1984; Costa and Shaffer 2012).

Estimates of FMR are central to understanding basic physiological and ecological processes, and the ability to link energy expenditure with behavior is crucial for conservation and management efforts (Gallagher et al 2015). These measurements are of particular interest for large, mammalian predators because they have high energy requirements that place considerable pressure on prey populations (Priddle et al 1998; Carbone et al 1999; Williams et al 2004; Smith et al 2015), and are often important in structuring ecological communities (Prugh et al 2009; Estes et al 2011; Ripple et al 2014; Roman et al 2014). There have been relatively few studies of FMR in free-ranging marine mammals (Costa and Gentry 1986; Costa et al 1989; Reilly and Fedak 1991; Arnould et al 1996; Boyd et al 1999; Costa and Gales 2000; Trillmich and Kooyman 2001; Costa and Gales 2003; Acquarone et al 2006), presumably due to the challenges associated with measuring metabolic rates in animals that spend most or all of their lives at sea. Empirical estimates from captive and free-ranging animals indicate that energy demands are quite variable among marine mammal groups (Costa 1991; Costa 1993; Costa 2009; Maresh 2014), with some groups adopting energetically expensive lifestyles (e.g., otariids - fur seals and sea lions) and others relying more on maximizing energy efficiency and not intake (e.g., phocids - true seals). The costs associated with foraging have only been estimated for a few species, and given the limited number of studies to concurrently measure FMR and behavior in free-ranging animals (Arnould et al 1996; Costa and

Gales 2000; Costa and Gales 2003; Williams 2004), it is generally not well understood how diving behavior affects inter- and intraspecific variability in energy expenditure.

Pinnipeds exhibit three primary dive patterns that are characterized by dive depth and position within the water column. Epipelagic (< 200 m) and mesopelagic (> 200 m) dives occur within the water column, whereas benthic dives are to the sea floor at any depth. Interspecific comparisons of energy expenditure in free-ranging otariids indicate that benthic diving may be energetically expensive, as species that are primarily benthic divers often have higher at-sea FMRs than epipelagic foragers (Costa and Gales 2000; Costa and Gales 2003). Costa et al. (2004) found that benthic-foraging otariids were more likely to approach or exceed their calculated aerobic dive limit than epipelagic-foraging species. The authors hypothesized that these species may therefore have limited flexibility to respond to changes in prey availability, which may be the cause of the slow population growth rates and declines observed for some benthic-foraging otariids (Costa et al 2004; Arnould and Costa 2006; Costa et al 2006).

Short-term energy balance is critical for female otariids because they have limited fat reserves, and in addition to an already expensive lifestyle, must cope with the added cost of lactation (Costa 1991). All female otariids share similar reproductive characteristics - during lactation, they are central-place foragers, alternating foraging trips to sea with periods of onshore nursing at the rookery (Costa 1991). This behavior not only makes female otariids a particularly tractable group for metabolic studies, but may also place considerable pressure on local prey populations and result in high levels of competition, as females are constrained in how far they can forage from the rookery. Intraspecific variability in foraging behavior is increasingly documented among female otariids from the same population (Villegas-Amtmann et al 2008; Lowther and Goldsworthy 2011; Kernaléguen et al 2012; Baylis et al 2015; Kernaléguen et al 2016), which may be a mechanism to reduce competition (Villegas-Amtmann et al 2013; Kernaléguen et al 2015). This has raised questions about the ecological and reproductive implications of behavioral variability that are largely unanswered, in part because the interplay between energy expenditure and behavior has only been investigated for a few species.

The overall goal of this study was to measure FMR and examine the relationship between energy expenditure and foraging behavior in adult female California sea lions, which are an abundant top predator in the California Current Ecosystem. To accomplish this, we measured FMR during a foraging trip to sea, and simultaneously used bio-loggers to collect data on at-sea movements and dive behavior. California sea lions are a particularly good model for investigating these relationships because they are flexible foragers, exhibiting multiple foraging strategies that encompass all three of the diving patterns characteristic of marine predators (Villegas-Amtmann et al 2011; Chapter 1). We discuss results in the context of previous studies to gain a better understanding of the drivers of intra- and interspecific variability in FMR in otariids in particular and other air-breathing marine predators in general.

2.3. Methods

Capture and instrumentation

Adult female California sea lions were captured at San Nicolas (*n* = 10; SNI) and San Miguel Islands (*n* = 6; SMI) in November and December of 2014. The majority of females were observed nursing a pup; the three remaining females were lactating at the time of capture but were never observed with a pup. Once captured in a net, females were weighed (± 0.1 kg), physically restrained, and anesthetized using gas anesthesia alone or in conjunction with an IM injection of midazolam (0.15 to 0.20 mg kg^{-1}) administered with atropine (0.02 mg kg^{-1}).

Females were instrumented with satellite tags and time-depth recorders of varying models (Wildlife Computers, Redmond, WA), and a VHF tag (Advanced Telemetry Systems, Isanti, MN). All tags were mounted on a neoprene base, attached to high-tension mesh netting using cable ties, and glued to the dorsal midline using a quick-setting epoxy. Despite the varying tag combinations, the overall weight and frontal surface area of the tags was generally similar among females. The combined package weights were less than 1% of body mass and approximately 2% of the cross-sectional area. Females were recaptured after approximately one foraging trip to sea – at this time we removed instruments, reweighed the animal, and collected blood samples (see below).

Field metabolic rate (FMR)

We used the doubly labeled water (DLW) method to estimate FMR (Nagy 1980; Speakman 1997). This method is one of the few available to estimate FMR in free-ranging animals, and has been validated against measures of food intake and O_2 consumption for pinnipeds (Costa 1987; Sparling et al 2008; Dalton et al 2014). The DLW method relies on changes in oxygen and hydrogen isotopes over time to estimate CO_2 production, and provides a single estimate of energy expenditure integrated across the entire measurement period. These measurements can also be used to calculate water influx, which can be used as a proxy for food intake (Costa 1987).

At the start of anesthesia, an initial blood sample was collected from the caudal gluteal vein to determine background isotope levels. This was followed by a single IV (*n* = 2) or IP injection (*n* = 14) of a weighed dose of sterile saline solution containing 99.8% ^{2}H and either 97% (~19 mL; SNI) or 10% ^{18}O (~130 mL; SMI). Females were held in a large dog kennel for 3-4 hours post injection to allow the isotope to equilibrate in the body water space; after this holding period, a blood sample was collected to determine the equilibration isotope concentrations before release. A final blood sample was collected at recapture to determine the final isotope enrichment. Serum and stock isotope solution samples were stored in plastic internal-threaded cryovials with an O-ring and wrapped in parafilm to prevent evaporation. All samples were stored frozen at -20 °C until analysis.

Serum and stock solution samples were analyzed for isotope concentrations at Metabolic Solutions Inc. (Nashua, NH). Mean isotope concentrations from triplicate measurements were used in the calculation of CO_2 production. Isotope dilution spaces were calculated using the plateau (initial) and scaling (final) methods (Speakman

1997). There are a variety of equations that can be used to calculate CO_2 production; we chose the two-pool Speakman et al. (1993) equation because it most closely approximates energy expenditure of otariids (Boyd et al 1995; Dalton et al 2014). Because estimates of CO_2 production are affected by the choice of equation, we also present estimates calculated using the Nagy (1980). A conversion factor of 23.6 kJ L^{-1} CO_2 was used to convert CO_2 production to energy consumption, which assumes that all fat and protein in the diet are oxidized (Costa 1987; Costa et al 1991). Water influx was calculated using the dilution space determined from ^{18}O and equations 5 and 6 in Nagy and Costa (1980).

A single estimate of CO_2 production is obtained from this method, however, there may be variability around this estimate because CO_2 production is calculated using the mean isotope enrichment of three triplicate measurements. We estimated this variability by recalculating CO_2 production for each female by mixing and matching individual triplicate measurements from the background, equilibration, and final serum samples (Speakman 1997). The mean and SD of these estimates were calculated from 10,000 simulations and used as an indication of the precision of our estimate of CO_2 production, and thus FMR.

The resulting estimate of FMR includes both the time an animal spent at sea and variable amounts of time onshore. To correct for this and calculate at-sea FMR, a regression equation between FMR and percentage time at-sea was used to 1) predict FMR for each animal given the percentage time spent at sea, 2) extrapolate a FMR for each animal if they spent 100% of their time at sea, and 3) add this extrapolated value to the difference between the actual FMR and predicted FMR to estimate at-sea FMR (Costa and Gales 2003). The percentage of time at sea was determined by summing the time spent in the water (determined via the wet-dry sensor on the TDR) and dividing by the total tracking duration (time of final blood sample - time of equilibration blood sample).

Stable isotopes

Blood samples were collected at the initial capture and recapture for stable isotope analysis. These samples were centrifuged and stored frozen in plastic cryovials at -20 °C until analysis. Plasma samples were analyzed for carbon (C) and nitrogen (N) stable isotopes as a proxy for the habitat use and diet of females over the time period of the metabolic measurement. We only used samples collected at recapture in statistical analyses, with the exception of one female from whom we used the sample from the initial capture because we were unable to obtain a plasma sample at recapture. To determine the appropriateness of this, females with paired samples (initial and recapture) were used to assess whether samples collected at the initial capture were representative of a female's behavior.

Samples were freeze-dried for 48 hours, homogenized, and weighed into tin capsules (0.5 ± 0.05 mg). They were analyzed using a Carlo-Erba NE2500 CHNS-O Analyzer coupled to a Thermo Finnigan DELTAplus XP Isotope Ratio Mass Spectrometer via a Thermo Finnigan ConFlo III at the University of California Santa Cruz Stable Isotope Laboratory. Results are expressed as a ratio using delta (δ) notation in units of parts per thousand (‰). Values were calculated from the equation

$\delta X = [R_{sample} / R_{standard}) - 1] \times 1000$ where $X = {}^{15}N$ or ${}^{13}C$ and $R = {}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$ in the sample and standard. The standard for C was Vienna-Pee Belemnite Limestone, and atmospheric N_2 (air) for N. Replicates of an internal laboratory standard were used to assess precision and were 0.04 ‰ for $\delta^{13}C$ and 0.07 ‰ for $\delta^{15}N$. Duplicate plasma samples were run for a subset of samples and were 0.02 ‰ for $\delta^{13}C$ and 0.03 ‰ for $\delta^{15}N$. The mean absolute difference in isotopes from the initial and recapture were 0.04 ‰ for $\delta^{13}C$ and 0.3 ‰ for $\delta^{15}N$ ($n = 7$). Paired *t*-tests indicated that neither isotope differed significantly between the initial and recapture ($\delta^{13}C$: $p = 0.93$, $\delta^{15}N$: $p = 0.14$).

Linking at-sea behavior with energetics

Satellite tags collected either ARGOS-quality locations or both ARGOS and GPS-quality locations. Location data were filtered using a speed and angle filter to remove erroneous locations. Hourly at-sea locations were predicted using a continuous correlated random walk (R package, *crawl*; ARGOS) or linear interpolation (GPS). These locations were used to calculate the mean transit rate (km hr^{-1}) and horizontal rate of travel (km day^{-1}). These two variables were similar with the exception that transit rate was calculated on an hourly basis and then averaged across the trip, whereas the horizontal rate of travel was calculated by dividing the sum of the total distance travelled at sea by the total time at sea. ARGOS locations were only used if no GPS data were available; this should not have affected comparisons as differences in movement statistics calculated using both location types are minimal (see Chapter 1).

Dive data, which were collected at 1 or 2 s intervals, were analyzed using a custom built-zero offset correction and analysis program in MATLAB (IKNOS, Y. Tremblay). Dives were defined as any dive 4 m or greater that lasted a minimum of 16 s. Dive data were used to both describe the average behavior of females at sea, and to characterize the foraging strategies and fine-scale behavior of females. First, we used all of the dive data to calculate mean values for the following variables: maximum depth (m), duration (s), bottom time (s), number of vertical excursions during the bottom phase of the dive (wiggles), dive rate (dives hr^{-1}), ascent and descent rates ($m\ s^{-1}$), efficiency ([bottom time/(dive duration + post-dive interval)]), intra-depth zone index (IDZ), and the percentage of time spent in different dive types. The IDZ is a measure of the tendency to dive repeatedly to a given depth (Tremblay and Cherel 2000). In addition, we calculated the percentage of time at sea spent diving, the vertical rate of travel ($km\ day^{-1}$), and an index of dive effort (Bowen et al 2001)

$$\frac{DE = \sum_i^n 2 * depth_i * duration_i}{TimeSea}$$

where *n* is the total number of dives.

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 sea floor), mesopelagic (≥ 200 m), and deep benthic (≥ 200 m and at or near the sea floor). 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 (~5,000 dives). The dive classifications and principal component scores from factors with eigenvalues ≥ 1 were used in a discriminant function analysis (DFA) 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 of the remaining 24,000+ dives. Predicted dive types were reclassified into the correct category if they did not meet the original category definitions (e.g., a dive with a depth of 201 m originally classified as epipelagic was reclassified as mesopelagic).

Because at-sea FMR is a single value that integrates a female's at-sea behavior, mean values (as described above) are generally assumed to be the most appropriate to examine the relationships between at-sea FMR and single variables. These mean values however may not accurately describe a female's behavior. For example, two females, one that dove exclusively to 40 m and one that spent 50 % of her time diving equally to depths of 10 m and 70 m, would have the same mean dive depth but not the same behavior. Additionally, dive variables tend to be strongly correlated with each other, precluding the ability to include multiple behavioral variables in the same model. To quantify behavioral differences among females, and assess whether there was any relationship between at-sea FMR and the overall behavior of females, we classified each foraging trip (trips > 6 hours) to one of the three foraging strategies exhibited by females as described in Chapter 1. For each foraging trip, we calculated the mean of the following variables: maximum day and night dive depths, bottom time, wiggles, efficiency, and intra-depth zone (IDZ) index. We also calculated the percentage of time at sea spent diving, percentage of dives during the day and night, percentage of epipelagic, benthic, and mesopelagic dives, and a diel index ([(mean day depth – mean night depth)/larger mean dive depth]). Lastly, a mean dive rate was calculated by averaging the dive rate for each bout (intensive periods of diving) across the foraging trip. Principal component scores for each foraging trip were predicted based on the data from Chapter 1. These scores were then used to predict the foraging strategy based on a DFA using data from Chapter 1.

Simple linear regressions were used to examine the relationship between at-sea FMR and each behavioral variable (including δ^{13}C and δ^{15}N values). To aid in interpretation of the linear regressions, Pearson correlations were used to examine the relationships among the different behavior variables (e.g., ascent rate vs. depth). We also used a multivariate approach to determine if females that had similar at-sea behavior also had similar at-sea FMRs. Distance matrices using Euclidean distances were calculated separately for the at-sea FMRs and PCA scores from the foraging strategy analysis. If a female had more than one foraging trip to sea, the average PCA score was used. PCA scores were weighted based on the variability explained by each dimension before the distance matrix was created. A Mantel test was used to examine the correlation between the energetic and behavior distance matrices. All statistical analyses were performed using R v.3.2.2. (R Core Group 2015). Mean values are shown ± SD unless otherwise stated.

2.4. Results

Metabolic rate measurements were obtained for nine females from SNI and all six females from SMI (Table 2.1). The remaining female from SNI was recaptured but not until 30+ days post injection when the isotopes had presumably been lost from her system. At SNI, six females were captured after one foraging trip to sea, one female was recaptured after two trips (C16), and the remaining two females were captured after 5+ trips to sea (C12 and C14). These two females made very short trips (~10 km) from the island, foraging during the day and returning to haul-out at night. At SMI, five females were recaptured after one foraging trip to sea; the remaining female (WAF2018) also made repeated short trips from the rookery, primarily foraging at night and returning during the day to an offshore island. All females were recaptured within 24 hours of returning to the rookery, but because they often arrived at night or early morning, most females were not recaptured until they had been ashore for at least six hours.

In general, females from SNI had longer foraging trips than females from SMI, which resulted in a longer measurement interval for SNI females (Table 2.1).

One female from SNI (C12) had isotope concentrations at recapture that were above, but close to background levels. This can result in erroneous estimates of energy expenditure if there is significant error in estimates of CO_2 production, or considerable variability in background isotope levels between the initial capture and recapture (background levels at recapture are assumed to be the same as initial). The variability in CO_2 production values for each animal from simulations was very small (SD ≤ 0.01), and mean CO_2 production values from simulations were within 0.0005 ml g^{-1} hr^{-1} of values used to calculate FMR. The variability among females in background isotope levels was also relatively small; background D^2 values differed by 0.32 ppm and O^{18} by 0.48 ppm. We therefore chose to include C12 in statistical analyses because (1) we were confident in our estimate of CO_2 production, (2) the slight variations in background isotope values between the initial and recapture would not have significantly affected the magnitude of the estimate (i.e., a high value would still have been a high value), and (3) inclusion did not affect any of the overall trends.

Field metabolic rates ranged from 1.52 to 5.48 W kg^{-1} with mean values of 3.90 ± 1.24 (SNI) and 3.48 ± 0.48 W kg^{-1} (SMI; Table 2.1). Females spent between 47 and 82% of the measurement interval at sea, resulting in estimated at-sea FMRs of 3.29 to 6.97 W kg^{-1} (Table 2.2). The range of at-sea FMRs was greater for females from SNI, but the overall mean at-sea FMR was similar between the two islands (SNI = 5.45 ± 1.08 W kg^{-1}, SMI = 4.92 ± 0.59 W kg^{-1}; one-way ANOVA, $F = 1.14$, $p = 0.31$). Water influx rates ranged from 83.0 to 174 ml kg^{-1} day^{-1} and mean values were very similar between the two islands (SNI = 131.7 ± 34.2 ml kg^{-1} day^{-1}, SMI = 132.1

± 29.2 ml kg^{-1} day^{-1}; one-way ANOVA, $F < 0.01$, $p = 0.98$). Water influx rates did not increase with at-sea FMR ($r = -0.21$, $p = 0.46$), indicating that high costs were not necessarily associated with high rewards.

Females from SNI primarily foraged around the northern Channel Islands, with the exception of the two females that stayed within ~10 km of the island (Figure 2.1A). In contrast, the majority of females from SMI foraged north of the Channel Islands along or just off the mainland coast (Figure 2.1B). There was considerable variation in the at-sea behavior of females, but they could generally be characterized into one of two foraging strategies (Table 2.2). Eleven females were classified into a mixed benthic strategy (primarily benthic and epipelagic dives), whereas the remaining four females were classified as deep-divers (primarily deep epipelagic and mesopelagic dives). Females that undertook multiple foraging trips to sea generally had similar behavior on all trips and clearly had one dominant foraging strategy.

There were no relationships between at-sea FMR and any of the behavioral variables ($r^2 = 0.001 - 0.14$, $p = 0.16 - 0.90$) when all of the females were included in the analysis. This changed, however, when we examined the relationship between at-sea FMR and behavior separately for the different foraging strategies. For the 11 females in the mixed benthic strategy, there were significant positive relationships between at-sea FMR and ascent ($r^2 = 0.45$, $p = 0.02$) and descent rates ($r^2 = 0.43$, $p = 0.03$), and marginally non-significant relationships for depth ($r^2 = 0.35$, $p = 0.06$) and duration ($r^2 = 0.30$, $p = 0.08$; Figure 2.2). The relationship between at-sea FMR and dive duration was strongly influenced by WAF2002; when she was excluded from the analysis this relationship became significant ($p < 0.01$), explaining 63% of the variability in at-sea FMR. All of the above dive variables were strongly correlated with each other ($r > 0.7$). We did not make any statistical comparisons for females in the deep-diving strategy because there were only four females in this group. The at-sea FMRs of deep-diving females were generally very similar despite some variability in behavior (Table 2.2).

Females that were more similar in their at-sea behavior did not necessarily have similar at-sea FMRs (Figure 2.3). This held true when all females were analyzed together ($r = -0.15$, $p_{sim} = 0.81$) and when separate correlations were performed for the two foraging strategies ($r_{benthic} = -0.04$, $p_{sim} = 0.40$; $r_{deep} = -0.24$, $p_{sim} = 0.59$). In general, females clustered into one of three categories of energy use - high, intermediate, or low at-sea FMRs (Figure 2.3A). Females using the mixed benthic strategy fell into all three categories, whereas females using the deep-diving strategy all had intermediate at-sea FMRs. The four females with the highest at-sea FMRs did cluster together behaviorally; however, they also clustered close to two other females that had either low or intermediate energy expenditure (Figure 2.3B).

2.5. Discussion

Intra- and interspecific comparisons of at-sea FMR

California sea lions in our study had a higher mean at-sea FMR than previously reported for this species (Costa et al 1991). When estimates were normalized for body mass, the mean at-sea FMR of California sea lions was slightly higher than Australian sea lions and northern fur seals, similar to Antarctic fur seals from the Arnould et al (1996) study, and slightly lower than New Zealand sea lions and Antarctic fur seals from the Costa et al (1989) study (Table 2.3). These results do not initially appear to support the hypothesis that benthic diving is energetically expensive, as California sea lions, which are typically considered epipelagic foragers, had similar at-sea FMRs as the two benthic-diving species. California sea lions actually exhibit a range of diving strategies, and females in our study had a relatively high proportion of benthic dives for an ‘epipelagic’ species (mean = 45%, range = 7 - 75%). This therefore does not necessarily refute nor support the hypothesis that benthic diving is an energetically expensive strategy.

The relatively high at-sea FMRs of sea lions in our study may have been due to reduced prey availability during late 2014, resulting in changes to time-energy budgets. Positive sea surface temperature anomalies were present in southern California in the fall of 2014, which eventually developed into a strong El Niño the following year (Leising et al 2014; Leising et al 2015). During this time period, pup weights at SMI were below the long-term average, indicating that the distribution or abundance of prey was not favorable for female sea lions. Subsequently, there was a large increase in the number of stranded, emaciated California sea lion pups in early 2015 (Leising et al 2015), suggesting that many females could not support their own energetic needs in addition to those of their pup. Females in our study were all in good body condition, but their pups generally weighed less than the long-term average of 7 month old pups (15.9 vs 25 - 28 kg), and the majority of females lost mass across the measurement period (Table 2.1). This mass loss, which is atypical for DLW studies with instrumented females (Arnould et al 1996; Costa and Gales 2000; Costa and Gales 2003), may have been due in part to fluctuations in milk mass as we did not know how long females had nursed their pups prior to the initial or recapture measurements. In spite of this, mass losses of some females were too great to be explained by milk delivery alone, and the at-sea behavior of females suggested that some might have had trouble finding food. In general, females travelled to similar foraging sites as in previous years (Melin et al 2008; Kuhn and Costa 2014), but in 2014 some but not all females spent more time at sea and appeared to work harder to find prey. For example, between 2005 and 2008 females at SNI had average trip durations of 5.4 days (mixed benthic strategy) or 3.5 days (deep-diving strategy) and spent approximately 39% and 23% of their time at sea diving, respectively (see Chapter 1). In the present study, the two females using the deep-diving strategy at SNI had trip durations of 5.7 (C3) and 8.2 days (C18), and on average spent 41% of their time at sea diving. Sea lions using the mixed benthic strategy also had increased trip durations (7.3 - 9.6 days, *n* = 3) and/or spent a greater proportion of time at sea diving (52 and 63%, *n* = 2); however, this trend did not hold for all sea lions.

The only previous study on California sea lion energetics was conducted during the 1982/1983 El Niño event (Costa et al 1991), yet females in our study still had higher at-sea FMRs than those reported in Costa et al (1991). This discrepancy may have been because the majority of energetic measurements actually occurred in 1984, when the El Niño conditions of 1982/1983 had been replaced by cooler, more productive waters. The mean at-sea FMR of the two females during 1983 was higher than during 1984, and is more similar to our estimates from 2014 (Table 2.3). Overall, these results suggest that energy expenditure of California sea lions increases during times of reduced food availability. A similar pattern has been documented for northern fur seals (*Callorhinus ursinus*) where females increased their foraging effort (but not trip duration) in response to inter-annual variation; however, females had higher food intake rates during years of increased effort, resulting in similar mass gains among years (Costa and Gentry 1986). For California sea lions, the increase in at-sea FMR may be because females had to work harder at finding food (as described above), and/or because females altered their foraging behavior to take advantage of available prey species (see below).

Energy expenditure and behavior

There were broad-scale behavioral differences among individuals (i.e., foraging strategies), which not only affected the energy expenditure of individuals, but also the relationships between at-sea FMR and behavioral variables. Females that used the deep-diving strategy all had at-sea FMRs that were intermediate between the lowest and highest values exhibited by the 11 females using the mixed benthic strategy, and we could not detect any relationships between at-sea FMR and behavior when females in both foraging strategies were analyzed together. This is not particularly surprising given that females using different foraging strategies likely target different prey, and that animals use a variety of mechanisms to conserve oxygen on long, deep dives. For example, Williams et al (2000) found that both pinnipeds and cetaceans relied on passive gliding or stroke-and-glide swim strategies during the descent and ascent phases of dives greater than 80 m. These swim strategies allow animals to take advantage of changes in buoyancy to conserve energy, and may partially offset the transit costs associated with deeper dives (Costa and Gales 2000; Crocker et al 2001). In addition to the use of energy-conserving swim strategies, all marine mammals exhibit a pronounced dive response characterized by extreme bradycardia (< 10 beats min^{-1}) on deep dives (Kooyman and Ponganis 1998). McDonald and Ponganis (2014) found that California sea lions only exhibited a true bradycardia on dives greater than 4 minutes, with dive heart rates that were less than resting rates in 68% (> 4 minutes) and 98% (> 5 minutes) of dives. In contrast, there was much more variability in heart rate profiles on shorter duration dives (> 3 minutes), and the percentage of dives with heart rates below resting was only 43 %. Further, the rate of oxygen consumption of captive sea lions generally fell below standard metabolic rates only when individuals were submerged for > 3 minutes (Hurley and Costa 2001). In our study, the mean dive durations of females using the mixed benthic strategy were typically less than 3 minutes compared with 4+ minutes for females using the deep-diving strategy. It is therefore likely that females using the deep-diving strategy have a greater dependence on strategies that conserve oxygen, which may help explain why the energy expenditure of these females did not appear to follow the fine-scale behavioral trends found for females using the other foraging strategy.

Fine-scale behavioral differences affected the energy expenditure of California sea lions using the mixed benthic strategy. We found positive relationships between at-sea FMR and a number of behavioral variables, including descent and ascent rates, and dive depth and duration. All of the predictor variables were strongly correlated with each other, making it difficult to disentangle which variables were driving this trend. Descent rates commonly increase with dive depth, which is likely due to the increased reliance on passive gliding or stroke-and-glide swimming during deeper dives (Crocker et al 2001; Watanuki et al 2003). Similarly, ascent rates increase towards the surface as animals come up from depth and experience positive changes in buoyancy, potentially due to lung re-inflation (Watanuki et al 2003). It is therefore more likely that dive depth and/or duration were driving the relationship with at-sea FMR, as faster descent and ascent rates would result from energy-saving swim strategies. Because this was a mixed foraging strategy consisting of both epipelagic and benthic dives, differences in depth and duration among females could have been due to changes in either dive type (i.e., an increase in the mean dive depth could be the result of deeper epipelagic or benthic dives, or both). The mean benthic dive depth and duration were both correlated with the overall mean values used in the analysis, but this was not true for epipelagic (or mesopelagic) dives. This suggests that the positive relationships between at-sea FMR and dive depth and duration were primarily driven by variability in the depth and duration of benthic dives.

There are two potential explanations for the increase in energetic cost with depth or duration of benthic dives. First, it is possible that females target different prey species at different depths, which could alter energy expenditure if prey required different capture or pursuit methods. California sea lions prey on some aggregating species that are found on the benthos during certain times of the day (e.g., market squid, *Doryteuthis opalescens*), which may require less energy to find and capture than larger, more cryptic species. We did not detect any relationship between at-sea FMR and δ^{15}N values, and there did not appear to be any consistent pattern in δ^{15}N values with benthic depth or duration. Despite this, we cannot exclude prey type as a potential contributing factor; δ^{15}N values are not synonymous with diet, and the large range of mean benthic dive depths (33 - 207 m) indicate it was unlikely that all females targeted the same prey species. An alternative hypothesis is that females undertaking longer dives spent more time in energetically expensive portions of the dive than during shorter dives. Our data appear to provide support for this hypothesis, as there was a strong positive correlation between bottom time and dive duration of benthic dives (Figure 2.4), and a weaker correlation between bottom time and depth. This indicates that on longer and often deeper benthic dives, females spend more time actively swimming at the bottom of the dive than on shorter and sometimes shallower dives. Although we did not detect any relationship between at-sea FMR and bottom time, the strength of this relationship was affected by characteristics of epi- and mesopelagic dives, and the presence of an outlier (WAF2002). There did appear to be a positive relationship between the two variables if we used mean bottom times of benthic dives instead of all of the dive types. These increased costs at the bottom of the dive may offset and even outweigh any savings from the energy-conserving swim strategies described above. Although this pattern has not been found for other otariids (see below), Sala et al (2014) found that Magellanic penguins (*Spheniscus magellanicus*) had the highest rate of energy expenditure during the bottom phase of dives, with total energy expenditure increasing linearly with the number of bottom wiggles.

We found relationships between at-sea FMR and behavioral variables that were different from previous studies on otariids, highlighting the need for additional studies that relate energy expenditure with behavior in this and other groups of diving mammals and seabirds. Costa and Gales (2000) found a negative relationship between at-sea FMR and dive depth for New Zealand sea lions, which was attributed to an increased reliance on burst-and-glide locomotion on deeper dives. New Zealand sea lions tend to have relatively long bottom durations that are independent of depth, and there is less variability in dive duration with depth than for California sea lions. This may mean that New Zealand sea lions have less flexibility to alter their behavior because they are already pushing their physiological limits, and therefore energy-conservation strategies have a greater influence on at-sea FMRs in this species. For Antarctic fur seals, energy expenditure was negatively related to the proportion of time at sea diving and the rate of vertical distance travelled, which the authors hypothesized was because animals that spent less time diving actually spent more time transiting between foraging patches (Arnould et al 1996). We did not detect any relationship between at-sea FMR and the proportion of time at sea spent diving for California sea lions; however, this may have been because factors other than just travel distance, such as prey type or availability, influence the proportion of time at sea diving. In addition, female Antarctic fur seals spent considerably less amount of time at sea diving (14 - 32%) than the sea lions in our study (26 - 63%), which also could explain interspecific differences. The relationship between at-sea FMR and behavior appears to be species and potentially context-specific, and caution should therefore be used in extrapolating these relationships to other species.

Energetic implications of foraging strategies

Quantifying the energetic tradeoffs among foraging strategies remains a key question in understanding how individual differences in behavior affect fitness. The foraging behavior of California sea lions can broadly be classified into one of three strategies (see Chapter 1), but females in our study largely did not use the shallow, epipelagic strategy. This is not surprising given that this species appears to be relatively flexible in their foraging behavior, with females switching among foraging strategies depending on prey availability. There was no clear separation in energy expenditure between the two foraging strategies, and generally no indication that females with similar overall behavior had similar rates of energy expenditure. There was also no evidence that females that expended more energy had a greater rate of food intake, although these results should be cautiously interpreted because the water content of prey affects water influx rate (Costa 1987). Because there is variability in behavior within a foraging strategy, the average energetic cost of a strategy likely varies through time. The direction and magnitude of this variation may be influenced by both the overall effort needed to find prey and the fine-scale behavior of females within each foraging strategy. For California sea lions, energetic tradeoffs among strategies (if they exist) are likely small compared with the influence of intrinsic characteristics (e.g., experience, resting metabolic rate) and fine-scale behavior on energy expenditure and prey intake. It is interesting to note that there was less variability in at-sea FMRs and water influx rates within the deep-diving strategy. This may have in part been due to differences in samples sizes among strategies; however, it is possible that females within this strategy actually experience intermediate, and less variable energetic costs than females using other foraging strategies.

Conclusion

Fine-scale differences in behavior can affect energy expenditure, but these relationships are complicated by broad-scale behavioral differences among individuals. As a result, there may not be a common set of variables that explain intraspecific variability in energy expenditure for air-breathing marine vertebrates that use multiple foraging strategies or dive types. For California sea lions, it appears that dive duration and/or depth are important in driving costs for benthic-diving females, but further studies are needed to determine which behavioral variables affect energy expenditure for females using the remaining two foraging strategies. Because there appears to be multiple behaviors that lead to high or low energy expenditure for California sea lions, and females have considerable flexibility to alter their behavior, seasonal and annual changes in prey availability may have a large impact on the energetics of this species. These results have implications for understanding and predicting energy expenditure in air-breathing marine vertebrates, especially for species that use multiple foraging strategies, and highlight the combined importance of energetic and behavioral studies on free-ranging animals.

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Table 2.1. Mass, pup status and mass, measurement interval, time at sea, total body water (TBW), water influx, and estimates of CO_2 production and field metabolic rate (FMR) of 15 adult female California sea lions from San Nicolas (SNI) and San Miguel Islands (SMI).

Sea lion ID	Initial mass (kg)	Final mass (kg)	Pup Mass (kg)	Interval (days)	Time at sea (days)	TBW (%)	H_2O Influx (ml kg^{-1} day^{-1})	CO_2 (ml g^{-1} hr^{-1})		FMR (W)		FMR (W kg^{-1})	
								Nagy	Speak	Nagy	Speak	Nagy	Speak
SNI													
C2	85.4	81.2	22.2	7.2	4.1	65.0	174	0.449	0.233	245.3	127.0	2.94	1.52
C3	78	75.4	Y	8.1	4.2	64.7	154	0.763	0.545	383.7	274.2	5.00	3.58
C8	59.8	63.4	13.0	9.0	6.6	66.6	172	0.997	0.743	402.5	300.4	6.53	4.88
C12	78.4	79.4	-	17.1	11.0	47.5	129	1.045	0.836	540.6	432.6	6.85	5.48
C14	86.2	76.0	-	11.9	8.4	64.0	83	0.774	0.628	411.5	334.1	5.07	4.12
C16	94.2	87	Y	14.1	8.8	63.5	130	0.880	0.678	522.7	402.9	5.77	4.45
C18	86	84.8	Y	11.1	7.3	65.1	139	0.713	0.510	399.1	285.6	4.67	3.34
C20	82.8	76.2	-	10.1	4.8	62.1	77	0.544	0.420	283.4	219.0	3.56	2.75
C22	95.4	83.2	8.3	11.2	7.3	63.0	127	0.969	0.763	567.4	446.7	6.35	5.00
SMI													
WAF2001	84.5	72.0	19.0	3.8	2.2	63.2	85	0.664	0.527	340.8	270.2	4.35	3.45
WAF2002	85.2	79.8	13.0	9.9	7.1	62.9	142	0.606	0.415	327.7	224.3	3.97	2.72
WAF2007	81.8	80.2	14.8	5.9	4.9	63.6	150	0.791	0.578	420.2	306.7	5.19	3.79
WAF2010	75.6	74.0	16.6	4.8	2.8	64.0	124	0.756	0.571	370.6	279.9	4.95	3.74
WAF2018	86.9	79.6	19.8	10.8	5.4	64.4	122	0.662	0.486	361.5	265.3	4.34	3.18
WAF2025	78.9	77.9	17.2	8.1	5.8	63.4	170	0.855	0.614	439.5	315.7	5.61	4.03

CO_2 production and FMR were calculated using equations from Nagy (1980) and Speakman et al. (1993)
Pup mass was only available for a subset of females; a pup mass of Y indicates the female was observed with a pup

Table 2.2. At-sea field metabolic rates (FMR) and a subset of behavioral variables for 15 adult female California sea lions. Females are separated by their overall foraging strategy, either a mixed benthic strategy consisting primarily of benthic and epipelagic dives, or a deep-diving strategy.

Sea lion ID	At-sea FMR ($W\ kg^{-1}$)		% Dive	Dive rate (dives h^{-1})	Depth (m)	Bottom time (s)	Duration (s)	Ascent rate ($m\ s^{-1}$)	Descent rate ($m\ s^{-1}$)	$\delta^{13}C/\ \delta^{15}N$
	Nagy	Speak								
Mixed Benthic										
C2	5.30	3.29	43.7	13.2	54.5	51.7	119.3	1.18	1.11	-17.1/17.2
C8	8.00	5.98	39.1	7.6	93.3	82.4	185.0	1.50	1.63	-16.7/18.0
C12	8.84	6.97	52.1	8.3	130.5	74.6	226.2	1.44	1.53	-17.3/17.4
C14	6.72	5.35	62.6	15.9	39.0	86.5	142.1	1.15	1.32	-18.1/17.6
C16	7.85	6.01	26.0	4.2	143.2	74.3	225.8	1.49	1.53	-17.1/18.1
C20*	6.49	4.95	30.2	8.2	41.1	65.3	132.3	1.24	1.43	-17.1/17.1
C22	8.27	6.44	36.1	7.5	92.2	67.1	173.3	1.45	1.44	-17.4/17.2
WAF2001	6.70	5.21	48.8	14.4	32.0	72.5	122.1	1.13	1.21	-17.0/17.5
WAF2002	5.58	3.93	34.2	6.1	74.1	102.3	202.3	1.17	1.33	-16.6/17.6
WAF2010	7.26	5.47	31.3	6.7	82.4	60.8	167.7	1.23	1.31	-16.6/17.3
WAF2025	7.18	5.20	45.4	10.4	41.9	85.8	157.2	1.07	1.06	-17.1/17.5
Deep-diving										
C3	7.29	5.29	39.9	6.0	161.7	82.4	238.0	1.44	1.61	-17.0/17.6
C18	6.56	4.75	41.9	5.9	188.9	63.5	255.5	1.45	1.59	-17.4/18.3
WAF2007	6.15	4.51	36.2	4.9	203.0	58.3	265.2	1.54	1.63	-16.3/17.5
WAF2018	7.10	5.25	37.3	7.9	105.2	46.8	169.6	1.02	0.90	-16.5/18.3

Dive rate, depth, bottom time, duration, and ascent and descent rates are mean values

% Dive is the percentage of time at sea spent diving

Isotope values were analyzed from plasma samples collected at recapture except for the female denoted by *

CO_2 production and FMR were calculated using equations from Nagy (1980) and Speakman et al. (1993)

Table 2.3. Summary of at-sea field metabolic rate (FMR) and relationships between energy expenditure and behavior for otariids. We present the mean ± SD, range, and mass-specific at-sea FMR (W kg$^{-0.75}$) for each study. If the relationships between at-sea FMR and behavior were investigated, we present the variable(s) and the direction of the relationship (positive or negative). Values are separated by the equations used to calculate CO_2 production, Nagy (1980) or Speakman et al (1993), as comparisons should not be made between equations.

Species	Mass (kg)	*n*	At-sea FMR (W kg^{-1})		Behavior
			Nagy	Speak	
California sea lion					
1983	78.5	2	7.82 ± 1.34 6.87 - 8.77 23.06		NA
1984	82.3	7	5.40 ± 1.02 3.99 - 7.18 16.07	NA	NA
2014	80.3	15	7.02 ± 0.97 5.30 - 8.84 21.01	5.24 ± 0.93 3.29 - 6.97 15.69	Dive depth (+) Duration (+) Asc./desc. rates (+)
Australian sea lion	69.3	20	7.05 ± 0.99 5.26 - 8.52 20.3	NA	No relationships
New Zealand sea lion	114.1	12	6.65 ± 1.09 5.20 - 9.31 22.6	NA	Dive depth (-)
Antarctic fur seal					
1984-1985	33.7	22	9.52 ± 2.58 5.66 - 17.49 22.94		NA
1991-1992	36.8	9	NA	6.34 ± 1.31 4.70 - 8.07 15.62	Prop. dive (-) Dive rate (-)
Northern fur seal	42.7	8	8.18 ± 2.10 5.43 - 11.30 20.9		NA

Data from this study, Costa et al (1991), Costa and Gales (2000), Costa and Gales (2003), Costa et al (1989), Arnould et al (1996), and Costa and Gentry (1986)

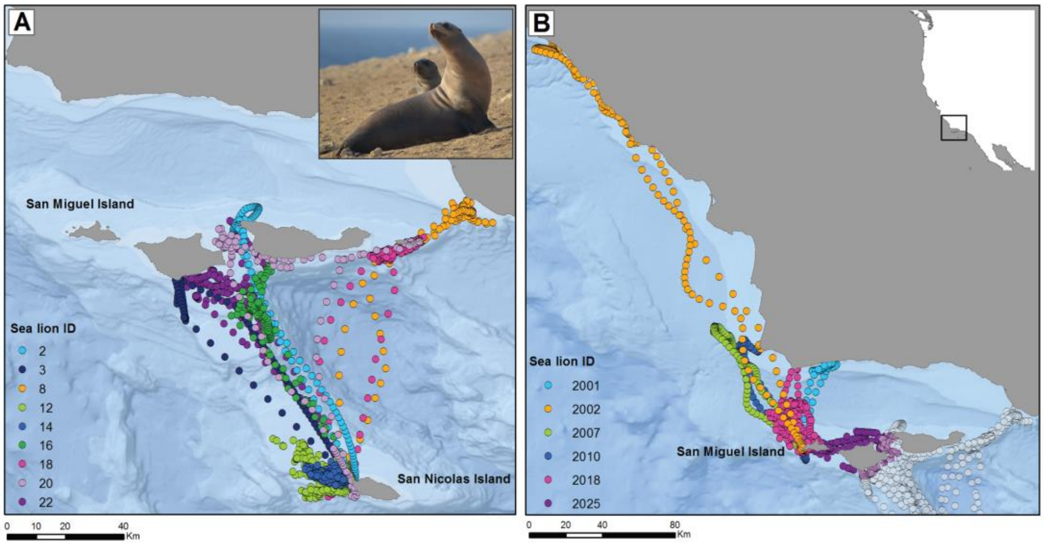


Figure 2.1. At-sea locations of adult female California sea lions from San Nicolas Island (A) and San Miguel Island (B). Females are represented by different colors in each plot. In B, tracks of females from San Nicolas Island are show in gray for reference.

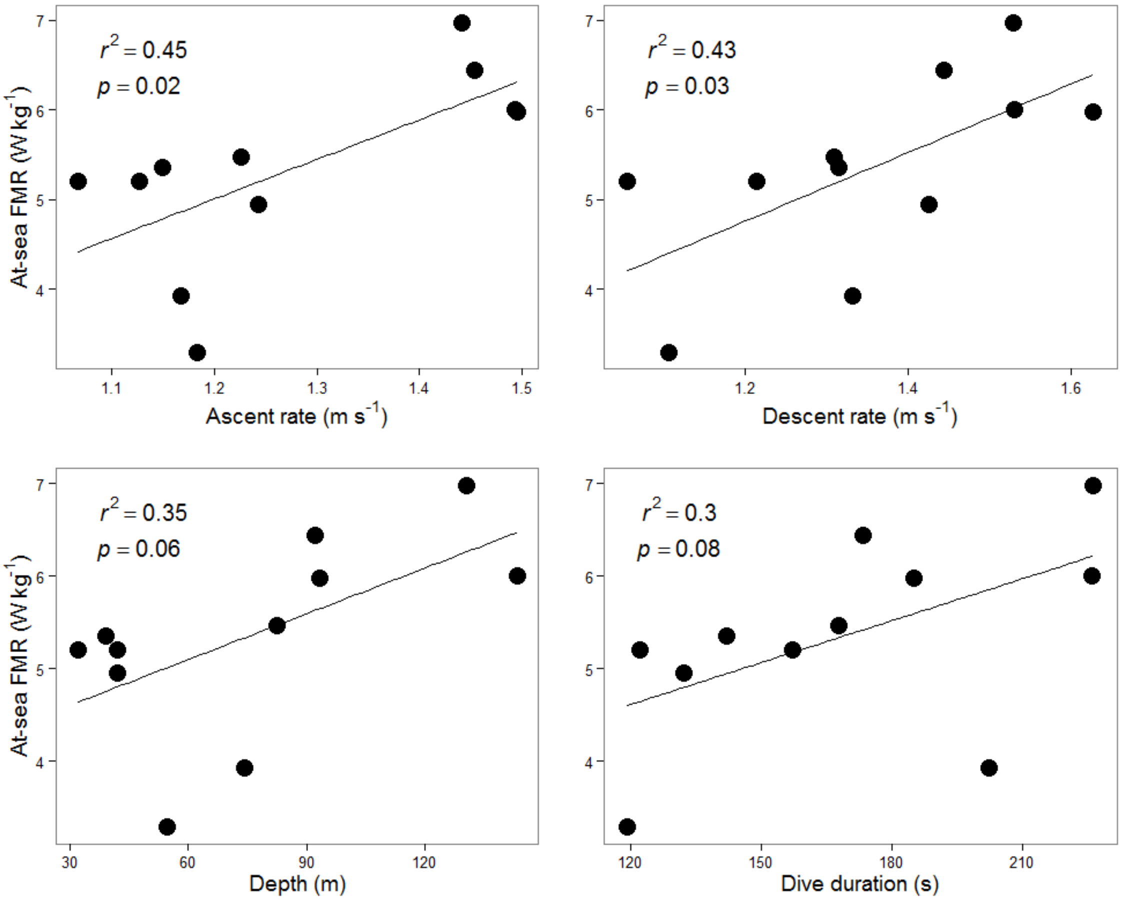
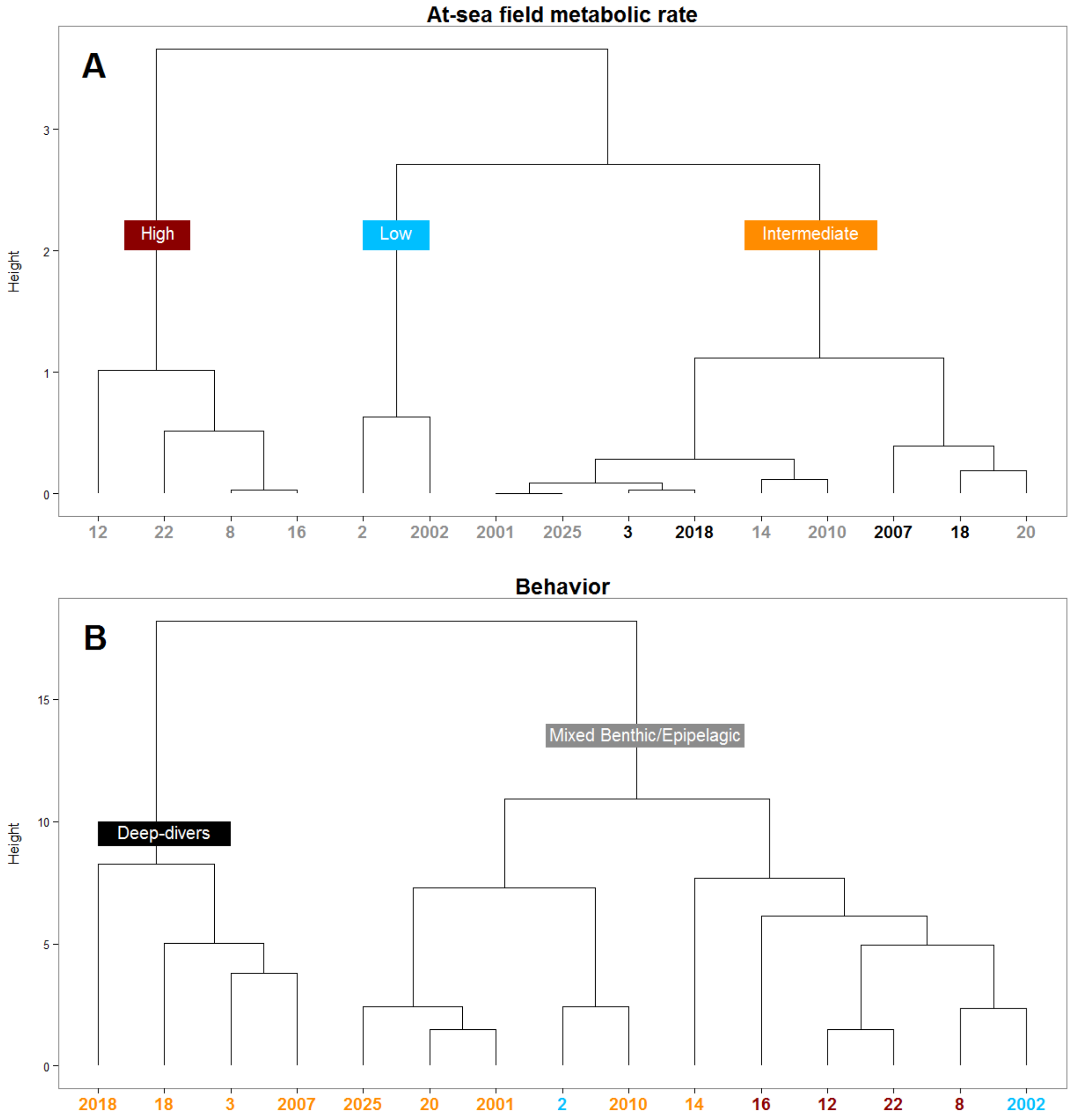


Figure 2.2. Relationships between at-sea field metabolic rate (FMR) and mean dive ascent rate, descent rate, maximum depth, and duration for the 11 adult female California sea lions that used the mixed benthic/epipelagic foraging strategy.



At-sea field metabolic rate

Behavior

Figure 2.3. Energetic (A) and behavioral (B) clusters based on distance matrices for 15 adult female California sea lions. In A, individual animals are colored by their foraging strategy (deep-diving or a mixed benthic/epipelagic strategy). In B, individual animals are colored by their energetic cluster (high, intermediate, or low).

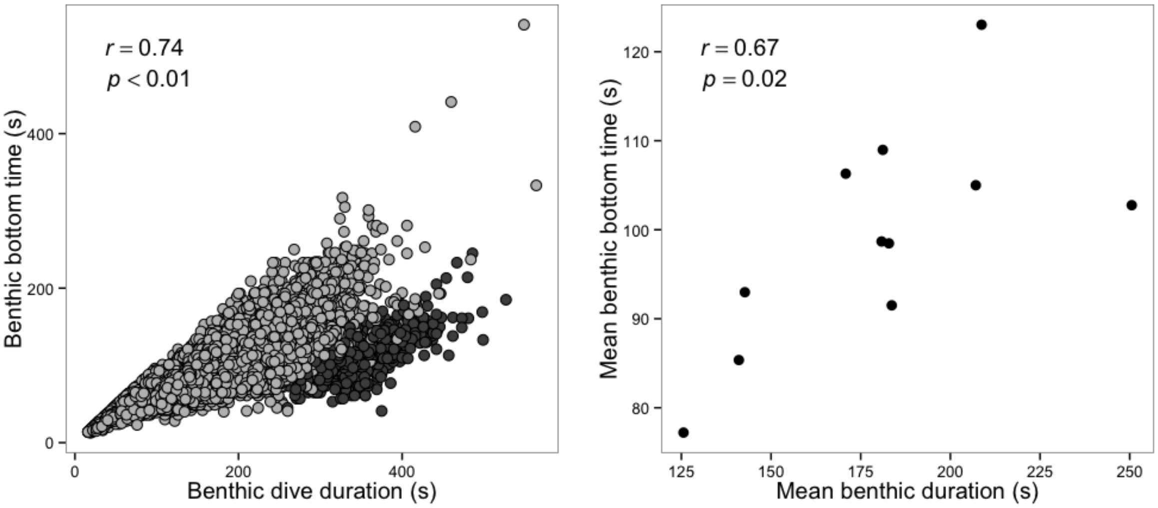


Figure 2.4. Relationship between bottom time and dive duration of benthic dives for 11 adult female California sea lions using the mixed benthic/epipelagic foraging strategy. Values for individual dives colored by depth (light gray < 200 m) are shown on the left, and mean values for each individual are shown on the right.

CHAPTER 3
Whisker growth dynamics of a temperate, non-migratory pinniped

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3.1. Abstract

Stable isotope analysis of whiskers is increasingly used to examine the long-term foraging behavior of pinnipeds, yet interpretation of isotopic values is complicated by a lack of data on whisker growth dynamics for most species. These data are necessary for understanding the amount of foraging information contained within whiskers, and determining if isotope values can be linked with specific time periods. The objectives of this study were to (1) determine the growth dynamics of California sea lions (*Zalophus californianus*) whiskers using photogrammetry of captive sea lions, and (2) estimate growth rates of whiskers collected from free-ranging sea lions using data derived from the captive study and from endogenous carbon isotope (δ^{13}C) oscillations within the whiskers. The latter method is commonly used for otariids, yet relies on the assumption that oscillations occur annually, which may not hold for a non-migratory species that exhibits considerable behavioral flexibility. The whiskers of captive sea lions grew linearly and were retained for multiple years, with growth rates that ranged from <0.01 - 0.18 mm day^{-1} and estimated whisker lifespans of 11+ years. The different methods used to estimate growth rates of whiskers from free-ranging sea lions generated overlapping ranges of growth rates, but estimates for individual sea lions did not necessarily overlap; growth rates derived from isotope oscillations were generally faster and more variable

than those derived from the captive data (0.06 - 0.15 vs 0.06 - 0.15 mm day^{-1}). Oscillations in δ^{13}C values were largely driven by movement among foraging areas close to the mainland coast and further offshore, with the drop in peak values likely corresponding to behavioral changes associated with reproduction. The best approach for estimating the whisker growth rates of individual free-ranging California sea lions was to use a combination of data collected from photogrammetry of captive sea lions and endogenous isotope oscillations within each whisker, largely because δ^{13}C oscillations did not always represent annual cycles. Collectively, these data contribute to a better understanding of otariid whisker growth dynamics, and facilitate the application of stable isotope analysis of whiskers for estimating the long-term foraging behavior of California sea lions.

3.2. Introduction

Stable isotope analysis has emerged as a powerful and cost-effective tool for describing the foraging behavior and habitat use of free-ranging animals. This method relies on the concept that stable isotopes of elements, most often carbon (C) and nitrogen (N), are transferred through food webs in a predictable pattern as a result of biochemical processes. Variation in the ratio of ^{15}N/^{14}N (δ^{15}N) typically reflects changes in trophic level, whereas ^{13}C/^{12}C ratios (δ^{13}C) are typically used as an indicator of foraging habitat (Kelly 2000; Newsome et al 2010). Tissues commonly used for stable isotope analysis reflect foraging behavior over different time scales (days to years), depending on the turnover or growth rate of the tissue (Crawford et al

2008). In contrast to blood and organs, the isotopic values of metabolically inert tissues, such as keratinized tissues and teeth, remain unchanged once grown. As a result, these archival tissues can be serially sampled to examine longitudinal patterns of isotope ratios, and used to quantify the long-term foraging behavior of individuals (Hobson and Sease 1998; Cherel et al 2009).

Stable isotope analysis of whiskers is increasingly used to quantify individual variation and dietary specialization in foraging behavior of pinnipeds, a diverse group of marine carnivores found in marine ecosystems worldwide (Hückstädt et al 2007; Cherel et al 2009; Eder et al 2010; Newland et al 2011; Lowther and Goldsworthy 2011; Lowther et al 2011; Hindell et al 2012; Hückstädt et al 2012; Kernaléguen et al 2012; Baylis et al 2015; Kernaléguen et al 2015a; Kernaléguen et al 2016). For most pinniped species, this is one of the few methods available to quantify the foraging behavior of individuals across multiple years, as bio-logging devices attached to the fur are limited by battery life and the annual pelage molt. Despite its utility, interpretation of isotope values in whiskers is complicated by a lack of understanding of whisker growth dynamics. These data are necessary for understanding the amount of foraging information contained within whiskers, and for linking isotope values with specific time periods. Results from the few studies on pinniped whisker growth indicate that dynamics differ at the family and potentially the species level. Phocid seals (true seals) exhibit asymptotic or irregular growth patterns, with whiskers that are in part shed annually (Hirons et al 2001; Greaves et al 2004; Zhao and Schell 2004; Beltran et al 2015), whereas the whiskers of otariids (sea lions and fur seals) appear to grow in a more linear manner over multiple years (Cherel et al 2009; Kernaléguen et al 2012; Kernaléguen et al 2015a; Rea et al 2015; Kernaléguen et al 2016). At present, limited data and remaining uncertainty concerning whisker growth in pinnipeds makes it difficult to determine when and how stable isotope analysis should be applied to studies of foraging behavior, and whether published growth values can be extrapolated to other species in the absence of species-specific measurements.

There are a variety of approaches that have been used to quantify whisker growth in pinnipeds. Direct methods include measurements of regrowth rates of clipped whiskers (Hirons et al 2001; Hindell et al 2012), and photogrammetry using long-term sampling of captive animals (Greaves et al 2004; Beltran et al 2015). Alternative methods rely on the use of stable isotope profiles along the whisker's axis to infer growth rates and whisker lifespan. Otariid whiskers often contain cyclic oscillations in isotope profiles that are assumed to represent annual cycles due to consistent spacing between oscillations, thereby allowing for an estimation of both whisker growth rates and the minimum age of the whisker. For species or age classes that lack cyclic isotope oscillations, the offset of isotope profiles from whiskers collected at two time periods can be used to infer growth rates by measuring the amount of new growth between the first and second collection (Hirons et al 2001; Hall-Aspland et al 2005; Rea et al 2015). Similarly, the administration and subsequent incorporation of exogenous tracers (e.g., glycine-enriched ^{15}N or ^{13}C) into new whisker tissue can be used to estimate growth rates by measuring the amount of new growth since the incorporation of the isotope tracer. All of these methods (except photogrammetry) rely on the assumption that whisker growth is constant, and therefore may result in erroneous estimates when growth is not linear. Photogrammetry provides a direct measure of the growth pattern, resulting in high-resolution growth data of many whiskers over relatively long time periods (months to years), but from a smaller number of individuals studied longitudinally.

The use of endogenous isotope oscillations within the whisker is the simplest method for estimating whisker growth rates of free-ranging animals, as it only requires the collection of a single whisker and does not require the recapture of individual animals. Cyclic oscillations within the whisker may occur because of predictable changes in animal behavior (e.g., seasonal shifts in foraging location or diet), or in the stable isotope composition at the base of the food web due to oceanographic changes (Cherel et al 2009; Kernaléguen et al 2012). This method has primarily been used to estimate growth rates of otariids that either inhabit regions with distinct seasonal variation in primary productivity (polar environments) or migrate across habitats that likely differ in their baseline isotope composition. Predictable behavioral shifts may largely be driven by reproduction, as oscillations have been detected in both male and female otariids (Cherel et al 2009; Kernaléguen et al 2012; Kernaléguen et al 2015b), but not juveniles (Rea et al 2015). The utility of this method for estimating growth rates of temperate, non-migratory otariids is largely unknown (but see Kernaléguen et al 2015c), particularly for species that exhibit considerable behavioral flexibility.

The goals of this study were to (1) determine the fine-scale whisker growth dynamics of California sea lions, and (2) establish the best method for estimating whisker growth rates of adult female California sea lions, which are flexible foragers found year-round in demersal and offshore habits of southern and central California. Specifically, we used photogrammetry of captive sea lions to determine the pattern of whisker growth, quantify whisker growth rates, and examine intra- and inter-individual variation in whisker growth rates. The growth rates of whiskers collected from free-ranging sea lions were estimated using three methods, two that relied on data derived from the captive animals, and a third that relied on endogenous isotope oscillations within whiskers, with the assumption that cyclic oscillations represented annual cycles. We assessed the best method for estimating whisker growth rates of free-ranging sea lions using a combination of bio-logging and isotope data to (1) determine the ecological drivers of variation in stable isotope values and (2) evaluate the assumption that endogenous isotope oscillation occur annually. This study not only contributes to a better understanding of the whisker growth dynamics of otariids and appropriate whisker sampling methods for species within this family, but also is an important step towards understanding the long-term foraging behavior of California sea lions.

3.3. Methods

Whisker growth dynamics of captive sea lions

Five adult California sea lions (four females, one male) living in human care participated in this study (Table 3.1). Subjects were housed at either Long Marine Laboratory at the University of California Santa Cruz or at Moss Landing Marine Laboratories. Animals were trained to cooperate in photogrammetry using operant conditioning with positive reinforcement (fish). Animals were trained to remain stationary with relaxed whiskers touching a plastic target while photographs were taken of both the left and right mysticial whisker beds (Figure 3.1). Photographs were taken using a Nikon COOLPIX AW100 placed at a fixed distance and angle from the animal, as in Connolly Sadou et al (2014) and Beltran et al (2015). A scale bar with 1 cm markers was placed within the frame of each photograph, either above the first row of whiskers or affixed to the measurement station. Photographs were taken at monthly intervals based on previous estimates that otariids whiskers grow relatively slowly, although the actual interval between sampling events depended on animal motivation and training schedules (Table 3.1).

The length of each whisker was determined from the scaled photographs using Image Processing and Analysis in Java software (Image J, NIH, http://imagej.nih.gov/ij/, 1997-2014). Measurements of whisker length using this method are within 1 mm of actual lengths (Connolly Sadou et al 2014). Individual whiskers were identified using the whisker bed maps from Connolly Sadou et al (2014). Photographs were selected for analysis based on the clarity of the photograph, position of the scale bar, and the visibility of whisker follicles and tips. Three to four photographs were analyzed per whisker bed; this typically resulted in one to three measurements per whisker for a sampling event as the follicle and tip were not visible in all photographs. Each whisker measurement was assigned a numerical value corresponding to the reader's confidence in the measurement (i.e., good or excellent). Missing whiskers were noted by follicle position but were not assigned a measurement value of zero because the month-long interval between sampling events resulted in uncertainty of the actual date of whisker loss.

Growth rates for each whisker were determined using weighted linear regressions of whisker length vs. time. The weighting factor was the confidence value and the estimated growth rate was the slope of the line. A minimum whisker lifespan (the age of the earliest deposited tissue) was estimated using the maximum whisker length and the growth equation from the linear regression for that whisker. We only estimated lifespans of whiskers that exhibited a strong positive relationship between length and time ($r^2 \geq 0.5$). The same approach was used to estimate the lifespan of whiskers that were lost during the study. Whisker measurements are presented in cm while growth rates are presented in units of mm day^{-1}.

We used a linear mixed effects model to determine the relationship between whisker growth rates and the length of the whisker, and estimate the amount of between- and within-individual variability. Individual sea lions were included as a random effect and maximum whisker length as a fixed covariate. We initially allowed individuals to differ in both their intercept and slope, but a log likelihood test revealed that models with and without a random slope were virtually identical; hence, the final model did not include a random slope. The analysis was restricted to whiskers with a strong positive relationship between length and time, and one sea lion (Rio) was excluded because she was frequently observed rubbing her whiskers on the floor of her enclosure.

Sample collection and isotope analysis

Adult female California sea lions were captured at San Nicolas (n = 10) and San Miguel Islands (n = 6) in November and December of 2014. A single whisker (generally the longest whisker) was pulled from either the left or right whisker bed while the animal was under gas anesthesia. During this initial capture, females were instrumented with a satellite tag and time-depth recorder to measure fine-scale foraging behavior (see Chapter 2). Female sea lions were recaptured 8 - 31 days later to recover instruments; at that time we also collected a blood sample for stable isotope analysis. Plasma was removed after centrifugation and stored in plastic cryovials at -20 °C. Whiskers were stored in paper envelopes at room temperature until analyzed for stable isotopes. Due to monetary constraints, we only analyzed whiskers from sea lions captured at San Nicolas Island.

Plasma samples from all 16 sea lions were freeze-dried for 48 hours and homogenized before analysis. Whiskers were sonicated for 15 minutes in de-ionized water and rinsed with petroleum ether to remove any exogenous debris. The total length of each whisker was measured before sectioning into ~3 mm segments. Tissue samples were weighed into tin boats (0.5 ± 0.05 mg) and analyzed for bulk C and N stable isotopes using a Carlo-Erba NE2500 CHNS-O Analyzer coupled to a Thermo Finnigan DELTAplus XP Isotope Ratio Mass Spectrometer via a Thermo Finnigan ConFlo III at the University of California Santa Cruz Stable Isotope Laboratory. Results are presented in delta (δ) notation and expressed as a ratio of the heavier to lighter isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$, $\delta^{13}C$ or $\delta^{15}N$) relative to either Vienna-Pee Belemnite Limestone (C) or atmospheric N_2 (N). Precision of an internal laboratory standard was 0.05 ‰ for $\delta^{13}C$ and 0.07 ‰ for $\delta^{15}N$. Duplicate samples of whisker segments differed by < 0.1 ‰ for both elements.

Whisker growth rates of free-ranging sea lions

We used data derived from the captive study and endogenous isotope oscillations to calculate three growth rate estimates for each whisker collected from free-ranging sea lions. These three estimates were obtained by (1) assuming that all sea lions exhibited the average growth rate from the captive study, (2) calculating whisker growth rate based on whisker lengths and the equation derived from the mixed effects model of growth rates and length from the captive study, and (3) estimating growth rates using a wavelet analysis of whisker $\delta^{13}C$ values. The equation from Connelly Sadou et al (2014) was applied to the whisker lengths of free-ranging sea lions to convert them from total whisker length (base + visible length) to visible length, which is what was measured in the captive study. The wavelet analysis, as described in Kernaléguen et al (2012), analyzes the frequency structure of isotope values through time (R package *WaveletComp*). We chose to use $\delta^{13}C$ values to calculate growth rates because initial plots of the data indicated that carbon isotope oscillations were often more distinct than nitrogen isotope oscillations; however, we did run wavelet analyses on δ^{15}N values for comparison as previous studies often use both isotopes to calculate whisker growth rates. The period of interest ranged from 3 mm to ½ the maximum length of the whisker (Kernaléguen et al 2012), and the significance of the periodicity was assessed using 1000 Markov simulations (Cazelles et al 2008). Growth rates were estimated based on the average frequency corresponding to the highest wavelet energy density, with the assumption that oscillations were annual.

The overall goal of using the three methods described above to calculate whisker growth rates was to identify the method that best approximated the actual growth rate of the whisker, with the understanding that the true value was unknown. We assumed that the use of endogenous isotope oscillations would provide a better estimate of the actual whisker growth rate than the two methods derived from captive data, as long as isotope oscillations represented annual cycles. To assess this assumption, linear models were used to examine the relationship between plasma δ^{13}C and δ^{15}N values and fine-scale foraging behavior to determine the ecological drivers of isotope variation, and therefore identify the most likely cause(s) of endogenous isotope oscillations. We used the mean dive depth, percentage of epipelagic and benthic dives, and a diel index to characterize the dive behavior of each sea lion (see Chapter 2). The interpolated positions of all dives that occurred within presumed foraging bouts were used to calculate the mean distance from the continental shelf and mainland California using ArcGIS. We ran all possible combinations of models (without interactions), with the exception that mean dive depth and the percentage of benthic dives were not allowed to occur in the same model together because they were correlated ($r > 0.6$). We used Akaike Information Criteria corrected for small sample sizes (AIC_c) to determine which variables were important in explaining the variability in stable isotope values. Results from this analysis were used to develop a set of criteria to identify the most appropriate growth rate for each sea lion, which is discussed below.

3.4. Results and Discussion

Whisker growth dynamics of California sea lions

A total of 6,662 measurements were collected on 321 whiskers from five sea lions over the study duration, which ranged from 245 to 399 days (Table 3.1). The maximum measured length of whiskers ranged from 0.4 to 19.0 cm, with variation in lengths among whisker positions and individuals. We detected significant, positive linear growth in 134 of the 321 whiskers that could be measured over at least three sampling events ($r^2 = 0.1 – 0.99$, $p < 0.05$; Figure 3.2, Appendix A.1). The remaining whiskers either had no detectable relationship between whisker length and time (40%), or significant negative relationships (18%). Estimated growth rates of whiskers with $r^2 > 0.5$ ranged from < 0.01 to 0.18 mm day^{-1}, with an average of 0.03 mm day^{-1} for whiskers of all lengths and 0.07 mm day^{-1} for whiskers > 7.0 cm. Results from the mixed effects model indicated that the within-individual variability was greater than the between-individual variability, and that whisker length was positively related to whisker growth rates ($F_{1,3.01} = 30.47$, $p = 0.01$).

Whisker retention rates were generally high for all sea lions. During the study, individuals lost zero to three whiskers ($n = 8$), with no noticeable spatial or temporal pattern to whisker loss. The mean delay between whisker loss and reemergence was 188 days, although this is likely an overestimate due to the difficulty in accurately measuring newly emerged sea lion whiskers. The minimum estimated lifespan of whiskers in the bed at the end of the study ranged from 0.2 to 10.7 years, with an average of 4.4 years. The estimated lifespan of the four whiskers lost during the study, for which growth rate estimates are available, indicate that these whiskers were 0.7, 3.5, 6.1, and 11.6 years at the time of loss. Estimates of whisker lifespan never exceeded the actual age of the animal, providing further confidence in our estimates of growth rates.

Whisker growth rates measured from the captive California sea lions encompassed the range documented for other otariid species, but the overall mean growth rate (0.03 mm day^{-1}) was less than published values for other adult otariids (0.05 - 0.14 mm day^{-1}, Table 3.2). These studies used cyclic oscillations in isotope profiles of one long whisker from each individual to infer growth rates of adults, but we were able to directly measure growth rates in individual whiskers that ranged in visible length from 0.2 - 19.0 cm. Because we found that longer whiskers grew at a faster rate, the interspecific differences between published values and mean growth rates reported for California sea lions in the present study can largely be attributed to the sampling methodology rather than species-typical differences. Indeed, the mean growth rate of longer whiskers (0.07 mm day^{-1}) was similar to mean growth rates of other adult otariids with similarly sized whiskers (0.05 - 0.09 mm day^{-1}; Table 3.2). The mean age of sea lion whiskers still retained in the bed was estimated at 4.4 years, which is consistent with other studies that have suggested multi-year retention due to the presence of multiple cyclic oscillations in isotope profiles (Cherel et al 2009; Kernaléguen et al 2012; Rea et al 2015). These results validate the assumption that otariid whisker growth is linear, which is central to other methods of estimating growth rates, and confirm that whiskers archive the foraging behavior of individual animals over a significant proportion of their lifespan.

There was considerable within-individual variation in the whisker growth rates of the sea lions, which was partially driven by differences in whisker length. The positive relationship we found between whisker growth rate and length indicates that otariids likely retain the shape of their sensory array through differences in growth rate and not differences in growth duration or retention time. Shorter whiskers towards the top or front of the whisker bed may therefore archive a similar amount of dietary information as longer whiskers, but into a smaller amount of tissue that is accrued more slowly. In addition to within-individual variation, there were slight differences in the maximum growth rates among sea lions. The two sea lions from Long Marine Lab (Ronan and Rio) had the slowest maximum growth rates (0.06 and 0.08 mm day^{-1}) compared with the three sea lions housed at the other facility (0.10 and 0.18 mm day^{-1}). These slight differences in growth rates may have been the cause of the observed differences in maximum whisker length among animals, which has also been suggested as an explanation for differences in the length of male and female fur seal whiskers (Kernaléguen et al 2012). Inter-individual variation in growth rates may be attributable to intrinsic differences among sea lions (e.g., metabolic rates), although we cannot rule out the potential effects of mechanical abrasion on growth rate measurements. There is some evidence that mechanical abrasion may have affected the growth rates of Rio, as she was observed rubbing her whiskers on her enclosure, and several of her whiskers appeared truncated and misshapen in photographs. Despite this, we feel that the overall effect of abrasion on whisker growth rates was minimal as it is unlikely that we would have detected positive linear relationships between whisker length and time under frequent abrasion.

Whisker isotope values and growth rate estimates of free-ranging sea lions

Whiskers of free-ranging sea lions varied in total length from 10.9 - 20.4 cm. The mean number (± SD) of whisker segments analyzed per sea lion was 33 ± 4.4, which was less than the total length of each whisker because segments close to the tip did not weigh enough to be analyzed. Isotope values within whisker segments ranged from -16.7 to -14.5 ‰ for δ^{13}C and 15.8 to 18.0 ‰ for δ^{15}N, with ranges that spanned 0.9 to 2.4 ‰ (δ^{13}C) and 1.1 - 2.2 ‰ (δ^{15}N) for individual sea lions (Appendix A.2). Initial plots of δ^{13}C and δ^{15}N values revealed that isotope values in the segment closest to the base were noticeably different from nearby whisker segments. This pattern has also been found in whiskers of harbor seals (Zhao et al 2006) and southern elephant seals (Hückstädt et al 2012), and because it is unlikely that these changes represent dietary information, the first segment (and for one sea lion the first and second) was removed before estimating growth rates.

Whisker growth rates estimated from the three methods ranged from 0.06 - 0.15 mm day^{-1}, resulting in whisker lifespans of 2.2 - 8.0 years. These growth rate and lifespan estimates were within the range of growth rates exhibited by the captive sea lions, which is not surprising given the captive data were used to generate a portion of these data. Although the three methods generated overlapping ranges of growth rates, estimates for individual sea lions did not necessarily overlap (Figure 3.3). Growth rates estimated from the wavelet analysis were generally more variable and faster than those estimated from either whisker length or the average growth rate. The slower growth rates estimated from captive data could be due to several factors, including mechanical abrasion as mentioned above, relatively few measurements of long whiskers, or simply because there is not a good relationship between growth rate and length for long whiskers when comparing among sea lions.

Ecological drivers of isotopic variation

Variability in plasma δ^{13}C values was mainly driven by broad-scale differences in foraging location, as the distance to the mainland coast was important in all of the top models (Table 3.3). The best model for δ^{13}C values explained 70% of the variability in the data, and also included the mean dive depth and mean percentage of epipelagic dives. There were three top models that explained between 58 to 63% of the variability in δ^{15}N values (Table 3.3). The percentage of epipelagic dives and the diel index were included in all three models for δ^{15}N, with mean dive depth and the percentage of benthic dives each included in one model. There were negative relationships between δ^{15}N values and the percentage of epipelagic dives and the diel index, which is an indicator of the strength of diel behavior (higher values represent large decreases in dive depth between day and night). Overall, these results indicate that δ^{13}C values increase as females forage closer to the mainland coast, and that δ^{15}N values increase as sea lions shift from shallow, epipelagic species towards prey found at deeper depths.

Whisker δ^{13}C and δ^{15}N *oscillations*

Sea lions exhibited significant periodicity in whisker δ^{13}C and δ^{15}N values ($p \leq 0.1$), although the amplitude and consistency of these oscillations varied among individuals and isotopes. For some sea lions, these oscillations occurred across the entire length of the whisker at similar periods, whereas others only had oscillations present across a portion of the whisker and/or at multiple periods (Figure 3.4). Oscillations of δ^{13}C and δ^{15}N values did not always occur at the same period(s), which would have resulted in conflicting growth rates for some individuals if both isotopes had been used to estimate growth rates. These results are largely in contrast to previous studies that have found that the period of isotope oscillations within adult otariid whiskers were generally consistent throughout the length of the whisker, and that δ^{13}C and δ^{15}N oscillations occurred at similar periods (Kernaléguen et al 2012; Kernaléguen et al 2015a; Rea et al 2015; Kernaléguen et al 2016). These inconsistencies are not particularly surprising given the relatively small foraging range and flexibility in dive behavior exhibited by adult female California sea lions.

For example, the dive behavior of female sea lions does not necessarily change when they forage in coastal vs. offshore areas, and they may target the same or similar prey types in different foraging areas. We would therefore not necessarily expect that shifts in δ^{13}C would result in corresponding shifts in δ^{15}N values, and vice versa.

Given the relationship between isotope values and fine-scale foraging behavior, peaks in δ^{13}C oscillations likely occur when female sea lions consistently forager close to the mainland coast. Adult female California sea lions give birth in June and July, alternating relatively short foraging trips (2 - 3 days) with periods of onshore nursing during the first few months of lactation (Melin et al 2000). The distance between San Nicolas Island and the mainland coast (~ 100 km) likely excludes the use of mainland foraging areas during this early lactation period, and we would therefore expect that δ^{13}C values would be relatively low during this time period. During late lactation, females undertake longer foraging trips and routinely use foraging areas along the mainland coast (Melin et al 2008; Kuhn and Costa 2014). Although they are non-migratory, female sea lions often leave the rookery when pups are weaned in March and April, heading northward to haul-outs close to the mainland. We suspect that the initial decline in δ^{13}C values corresponds with the onset of pupping, and that the gradual increase in δ^{13}C values reflects the ability of females to undertake longer foraging trips during late lactation. There may be a slight offset between the actual timing of these events and when it is reflected within the whisker because of the turnover of isotope values in blood and the slow grow rate of whiskers. The lack of annual isotope oscillations for some sea lions is not particularly surprising given that (1) spatial use varies among individuals and with prey availability (Melin et al 2008; Kuhn and Costa 2014), and (2) sea lions may not give birth every year, particularly following periods of poor prey availability (Melin et al 2012).

Selection of growth rate estimates

The presence of annual and multi-year cyclic oscillations in δ^{13}C values indicates that wavelet analysis can, but may not always, be an appropriate method to estimate whisker growth rates for individual California sea lions. Thus, two criteria were used to determine which of the three methods (the average growth rate of captive sea lions, the relationship between whisker growth rate and length derived from captive sea lions, or the wavelet analysis) best approximated the actual whisker growth rate of each sea lion. Growth rates obtained from all three methods were used to timestamp each whisker section, with the assumption that the most recent growth had occurred one week before the whisker was plucked. The timing of pupping (June - July) was overlaid on the temporal record of δ^{13}C values to examine which method resulted in the best temporal overlap between peak oscillations and pupping (Figure 3.5). To further discriminate among methods, we examined how the oscillation with the greatest relative magnitude varied temporally among sea lions (i.e., did the highest peak for each sea lion occur within the same year). This was based on the assumption that inter-annual changes in baseline δ^{13}C values should be reflected in the isotope values of all sea lions, regardless of behavior.

The wavelet analysis was the best of the three methods for approximating growth rates of six sea lions, including one sea lion (C8) that had oscillations at multiple periods (Figure 3.5). The remaining sea lions had growth rates that were best approximated by the average growth rate (*n* = 4). This resulted in final growth rate estimates of 0.06 - 0.12 mm day^{-1} ($\bar{x}$ = 0.08 ± 0.02 mm day^{-1}), with whisker archiving between 2.6 - 5.6 years of foraging information ($\bar{x}$ = 4.5 ± 1 years; Table 3.4). The oscillation with the greatest magnitude generally occurred around pupping in 2013 (Figure 3.5), which is consistent with environmental conditions during that time period. The spring of 2013 was characterized by strong upwelling that resulted in anomalously high chlorophyll concentrations in central California (Leising et al 2014). These types of highly productive oceanographic conditions are correlated with increases in baseline δ^{13}C values (Woodworth et al 2004; Miller et al 2008), which would be reflected in the isotopic composition of higher trophic levels. There was not only temporal coincidence between environmental conditions and elevated δ^{13}C values, but also in the temporal absence of oscillations among individual (i.e., sea lions tended to lack oscillations in the same year), lending confidence to our selection method for estimating whisker growth rates of free-ranging sea lions.

Conclusion

Stable isotope analysis of whiskers is a valuable tool for quantifying the long-term foraging behavior of pinnipeds, although the utility of this method depends on both the pattern of growth and the ability to estimate growth rates of free-ranging animals. Our results indicate that California sea lion whiskers do grow at a constant rate, thus growth rates can be used to assign a deposition time to whisker segments and link changes in isotope values with ecological and life history events for this species. Current whisker sampling methods for otariids involving the collection of one long whisker appear appropriate, as we found longer whiskers accrued dietary information at a faster rate than shorter whiskers. In the absence of species-specific growth rates, the growth rate from another species with similarly sized whiskers appears to be an appropriate substitute for estimating the average amount of foraging time represented in whisker segments. The best approach for estimating the whisker growth rates of individual free-ranging California sea lions was to use a combination of data collected from photogrammetry of captive sea lions and endogenous isotope oscillations within each whisker. This was largely because California sea lions did not always exhibit consistent periodicity in δ^{13}C oscillations, and even when they did, it was not always a good indicator that oscillations represented annual cycles. Collectively, these results indicate that estimates of whisker growth rates are possible despite the non-migratory nature and behavioral flexibility of this species, and that stable isotope analysis of whiskers can be used to quantify the long-term foraging behavior of California sea lions.

3.5. Acknowledgements

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Table 3.1. Demographics of the captive animals in the study and summary information of photogrammetry sessions. Duration is the number of days over which whisker measurements were collected, sessions refers to the total number of photogrammetry sessions per individual, frequency is the most common time interval between sampling events, and interval is the mean number of days ± SD between sampling events.

Sea lion	ID	Age (yr)	Sex	Duration	Sessions	Frequency	Interval
Rio	NOA0004827	29-30	F	399	13	Monthly	37 ± 18
Sake	NOA0003640	27-28	F	369	8	Bi-monthly	58 ± 7
Nemo	NOA0006047	18-19	M[a]	351	8	Bi-monthly	54 ± 25
Cali	NOA0006156	11-12	F	245	6	Bi-monthly	54 ± 32
Ronan	NOA0006602	6-7	F	385	13	Monthly	36 ± 17

[a] Neutered male

Table 3.2. Summary data on whisker growth dynamics for otariids separated by species and study. Mean values ± SD are presented when available for growth rates and whisker length of study animals. The ranges of mean growth rates or whisker lengths of study animals are presented when overall means were not available. Data were separated by age class and sex when possible and abbreviations are as follows: A = adult, SA = subadult, YoY = young of the year, Fe = fetus, M = male, and F = female. Growth patterns are only presented from studies that specifically discussed the pattern of growth. Data from this study are shown in bold.

	Rate (mm day^{-1})	Length (cm)	Pattern	Method	Citation
Steller sea lion	0.15 ± 0.05 (A)	NA	Linear	Isotope oscillations	Rea et al (2015)
	0.20 ± 0.03 (SA)	NA	Linear	Isotope oscillations	Rea et al. (2015)
	0.29 ± 0.09 (YoY)	NA	NA	Isotope matching	Rea et al. (2015)
	0.24 ± 0.02 (Fe)	NA	NA	Multiple[a]	Rea et al (2015)
	0.10 - 0.14 (A)	9.0-10.0	Linear	Isotope oscillations	Hirons et al (2001)
	0.05-0.09 (A)	NA	NA	Isotope tracers	Hirons et al (2001)
	0.14 - 0.17 (SA)	NA	NA	Clip and regrow	Hirons et al (2001)
Antarctic fur seal	0.05-0.08 (F)	13.2 ± 3.8	Linear	Isotope oscillations	Kernaléguen et al (2015a)
	0.10 ± 0.04 (F)	NA	NA	Clip and regrow	Walters (2013)
	0.14 ± 0.02 (M)	21.3 ± 6.4	Linear	Isotope oscillations	Kernaléguen et al (2012)
	0.08 ± 0.02 (F)	14.6 ± 4.6	Linear	Isotope oscillations	Kernaléguen et al (2012)
	0.13 ± 0.02 (M)	8.4 -33.3	Linear	Isotope oscillations	Cherel et al (2009)
Subantarctic fur seal	0.09 (F)	13.2 ± 3.8	Linear	Isotope oscillations	Kernaléguen et al (2015a)
	0.14 ± 0.04 (M)	19.1 ± 4.9	Linear	Isotope oscillations	Kernaléguen et al (2012)
	0.09 ± 0.02 (F)	13.3 ± 2.7	Linear	Isotope oscillations	Kernaléguen et al (2012)
Australian fur seal	0.09 ± 0.03 (F)	13.0 ± 2.7	Linear	Isotope oscillations	Kernaléguen et al (2016)
	0.09 ± 0.03 (F)	16.5 ± 3.0	Linear	Isotope oscillations	Kernaléguen et al (2015b)
	0.17 ± 0.04 (M)	21.0 ± 4.5	Linear	Isotope oscillations	Kernaléguen et al (2015b)
California sea lion	**0.07 ± 0.04 (A)**	**11.7 ± 3.8**	**Linear**	**Photogrammetry**	**This study**
	0.03 ± 0.03 (A)	**3.9 ± 1.9**	**Linear**	**Photogrammetry**	**This study**
	0.09 ± 0.02 (A)	**13.5 ± 2.8**	**NA**	**Multiple[b]**	**This study**

[a] Growth rates were calculated using either isotope oscillations or by dividing whisker length by the estimated age of the animal

[b] Growth rates were calculated using isotope oscillations, the average growth rate captive sea lion whiskers, or the relationship between whisker growth rate and length

Table 3.3. Model output for all models within 2 ΔAIC_c of the top model. The intercept-only model is shown for comparison

Model	*k*	logLik	AIC_c	ΔAIC_c	*w*	r^2
$\delta^{13}C$						
Depth + DistMain + Epipelagic	5	1.88	12.22	0.00	0.22	0.70
DistMain	3	-2.50	12.99	0.77	0.15	0.58
DistMain + Benthic	4	-0.74	13.11	0.88	0.14	0.61
Depth+DistMain	4	-0.99	13.62	1.40	0.11	0.60
DistMain + Epipelagic	4	-1.04	13.71	1.49	0.10	0.60
Intercept-only	2	-9.50	23.92	11.70	0.00	0.00
$\delta^{15}N$						
Diel + Epipelagic	4	0.01	11.63	0.00	0.30	0.58
Depth + Diel + Epipelagic	5	1.74	12.52	0.90	0.19	0.63
Diel + Benthic + Epipelagic	5	1.21	13.58	1.96	0.11	0.61
Intercept-only	2	-8.02	20.97	9.34	0.00	0.00

DistMain is the distance to the mainland coast

Table 3.4. Summary data on length (cm), estimated growth rate (mm day^{-1}), and lifespan (years) for whiskers collected from ten free-ranging adult female California sea lions. Growth rates represent the best fit estimate from either a wavelet analysis (Wavelet) or the average growth rate obtained from captive sea lions (Average).

Sea lion ID	Length	Growth Rate	Lifespan	Method
C2	11.0	0.07	4.3	Average
C3	20.4	0.10	5.4	Wavelet
C5	12.0	0.07	4.7	Average
C8	10.9	0.06	4.7	Wavelet
C12	12.9	0.10	3.6	Wavelet
C14	14.8	0.08	4.9	Wavelet
C16	11.5	0.12	2.6	Wavelet
C18	12.8	0.09	3.7	Wavelet
C20	14.9	0.07	5.8	Average
C22	14.3	0.07	5.6	Average

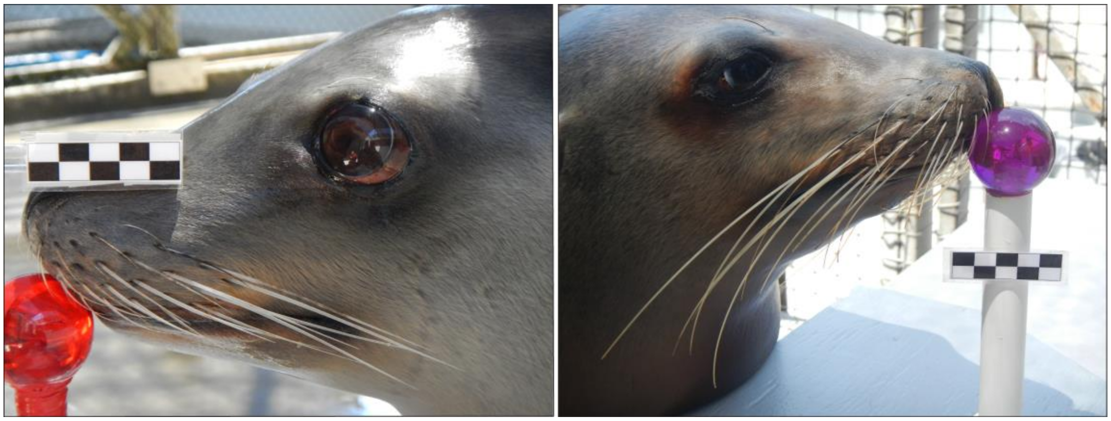

Figure 3.1. Photogrammetry configurations used for California sea lions.

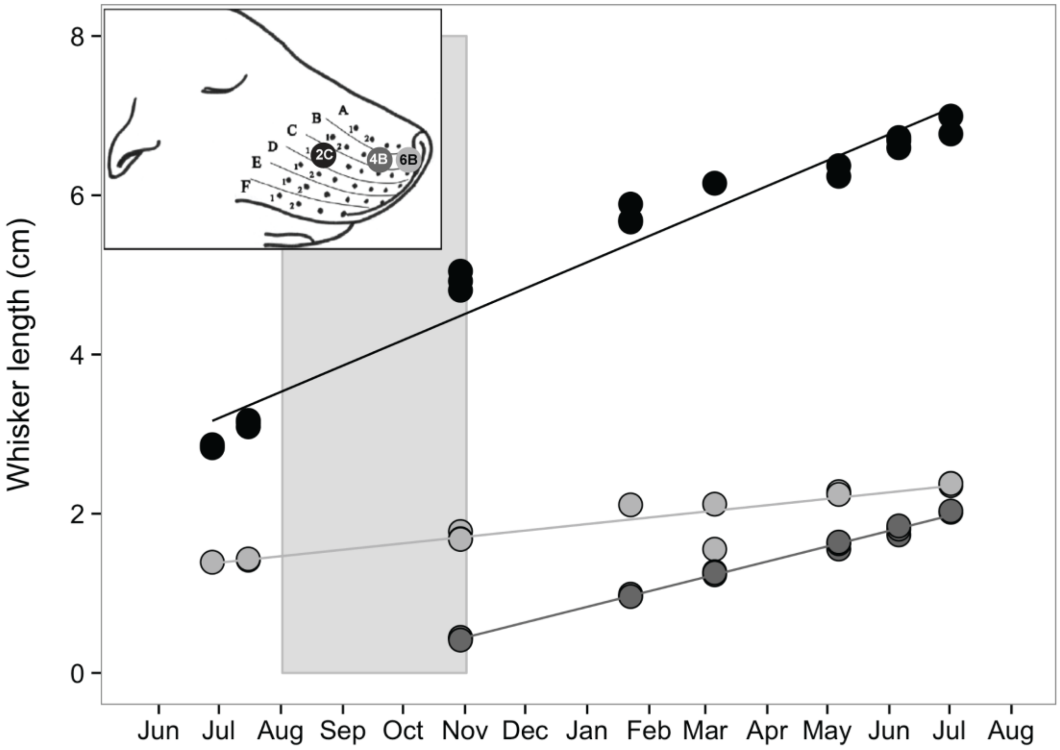

Figure 3.2. Whisker length vs. time depicting linear growth of three California sea lion whiskers. The position of each whisker on the bed is shown in the inset bed map from Connolly Sadou et al (2014). The gray box represents the time period of the annual pelage molt.

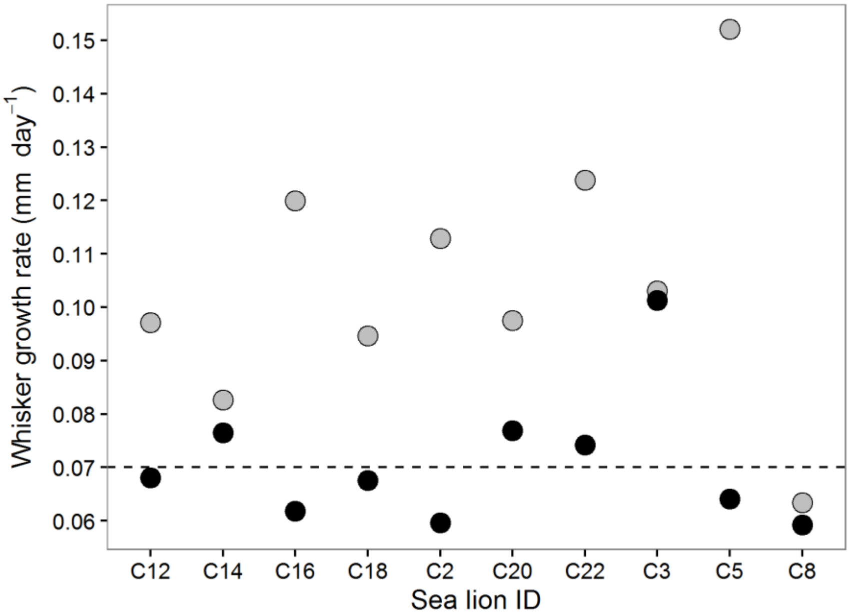

Figure 3.3. Whisker growth rates of 10 free-ranging adult female California sea lions. Growth rate estimates were determined using a wavelet analysis of δ^{13}C values (gray) or whisker lengths (black). The average growth rate is shown by the dotted line.

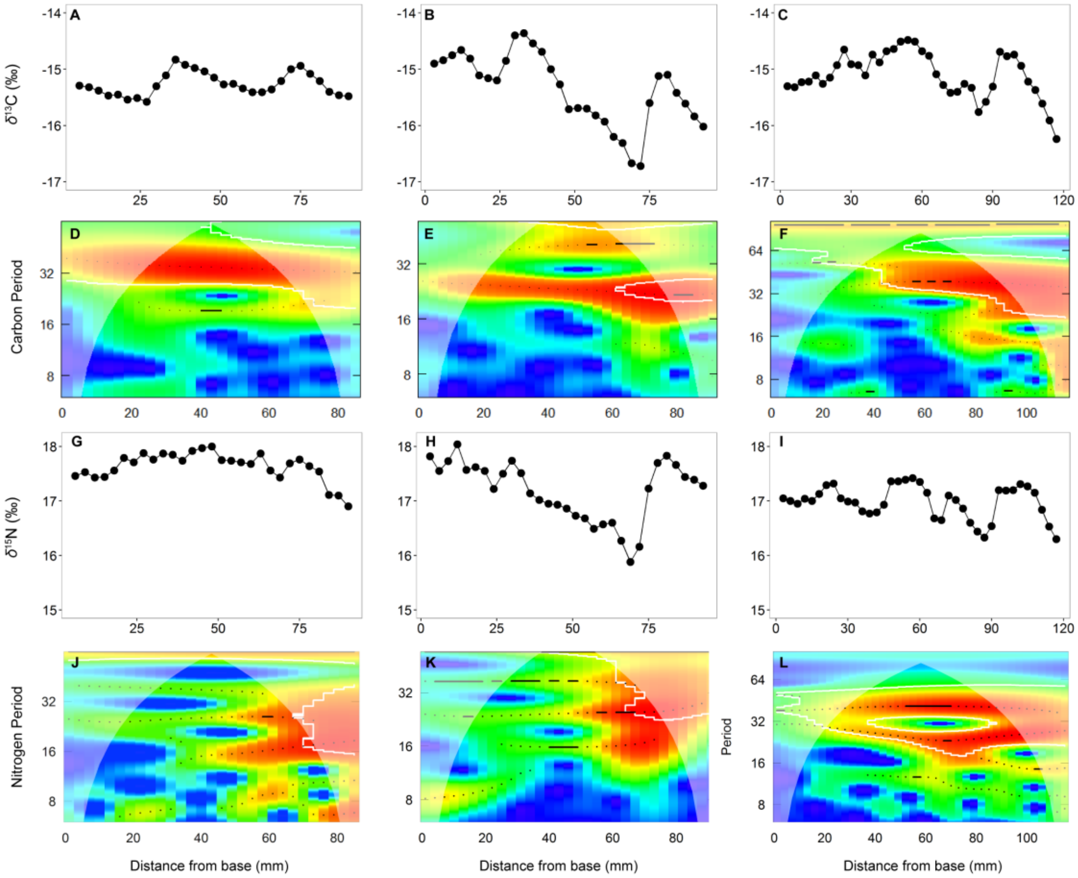

Figure 3.4. Variation in δ^{13}C (A - C) and δ^{15}N (G - I) values across the length of the whisker for three California sea lions, and power spectrum plots from the wavelet analysis indicating the periodicity of oscillations within each whisker (D - F, J - L). Warmer colors correspond to periods with greater power, with significant periods denoted by the white line. The opaque region of the plot corresponds to areas influenced by edge effects.

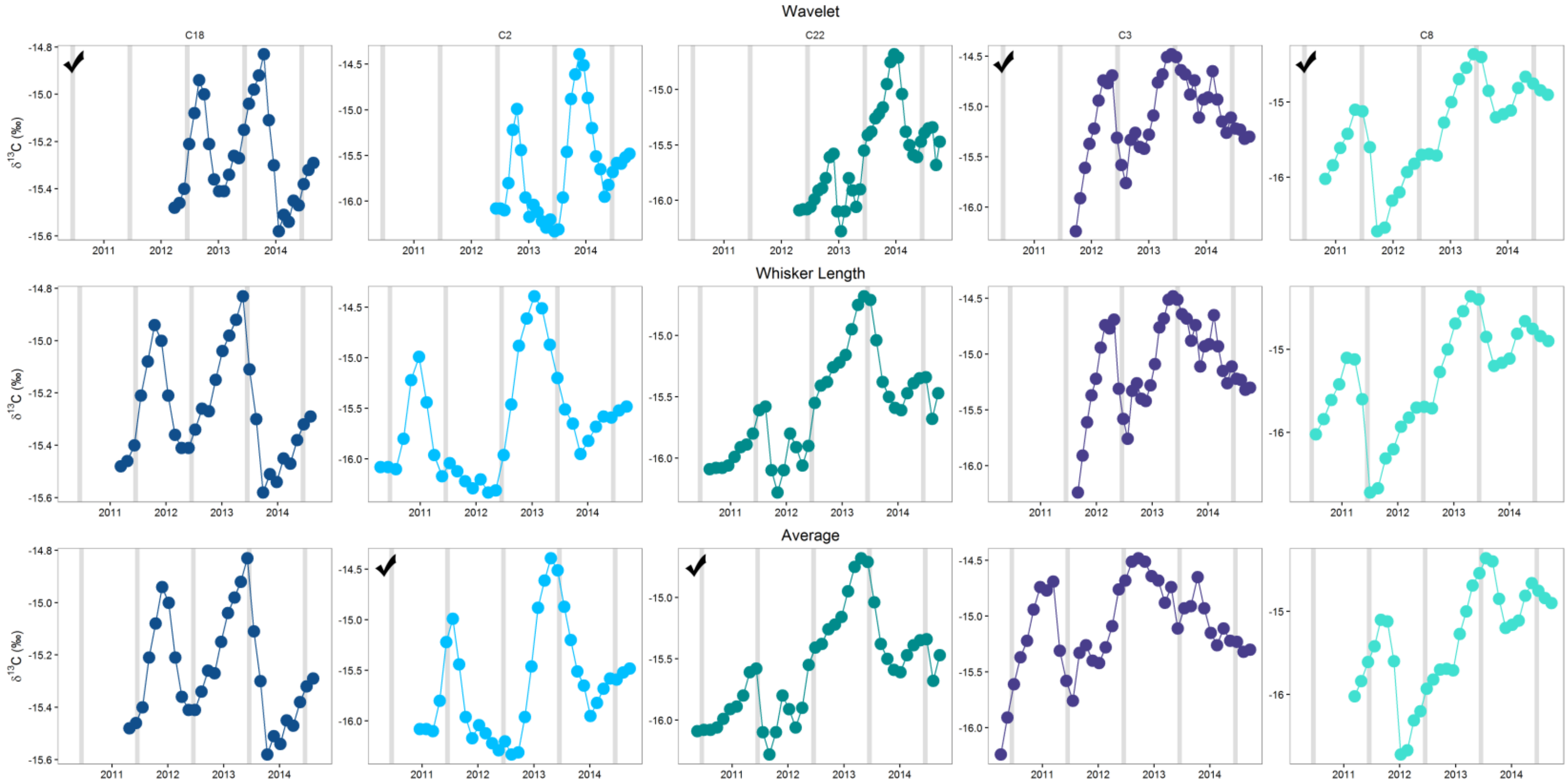

Figure 3.5. Temporal variation in δ^{13}C values of whiskers collected from five free-ranging adult female California sea lions. Each column represents an individual sea lion, and each row a different method for estimating whisker growth rates. The gray bars in each subplot represent the time of pupping (June - July). The check mark corresponds to the method that best approximated the whisker growth rate of that individual sea lion. Note that the scale of the x-axis differs among subplots.

CHAPTER 4
Population- and individual-level consistency in foraging behavior of a generalist marine predator

McHuron, E.A., and Costa, D.P.

4.1. Abstract

Consistent intraspecific differences in foraging behavior are widespread across a variety of taxonomic groups, and are not only ecologically relevant but also may affect the ability of individuals and populations to adapt to environmental changes. The purpose of this study was to examine consistency in foraging behavior of a generalist marine mammal that inhabits an ecosystem characterized by seasonal and annual fluctuations in the availability of prey resources. We used a combination of bio-logging and stable isotope data to quantify the repeatability of fine- and broad-scale foraging behavior of adult female California sea lions across multiple time scales, and examine whether individual sea lions differed in their behavioral consistency. California sea lions were repeatable in fine- and broad-scale behaviors across a period of several months to several years. The strength of behavioral consistency varied within and among fine-scale behavioral categories, with dive behaviors generally more repeatable than variables related to foraging effort or movements. Repeatability estimates of fine-scale foraging behaviors generally decreased as sea lions were tracked across longer time periods, likely in response to changes in prey patch characteristics and distribution. Sea lions also varied in the strength of behavioral consistency at the individual-level, but individual consistency in dive behavior was largely independent of foraging site fidelity. Prey type and behavior is a likely driver of sea lion behavioral consistency at both the population-

and individual-level, although it remains unknown what factors actually drive individual sea lions to choose different prey types. The decreasing strength of behavioral consistency with time suggests that sea lions do alter their behavior in response to environmental changes; however, behavior was largely consistent across longer time scales that encompassed several periods of reduced prey availability. This suggests that many sea lions stick to what they know even in the face of environmental changes, which raises questions about how the strategies that individual animals use to cope with environmental variability affect survival and reproductive fitness.

4.2. Introduction

Consistent individual differences in behavioral traits are increasingly documented across a wide variety of taxonomic groups, with implications for both ecology and evolution (Réale et al 2007; Bell et al 2009; Wolf and Weissing 2012). Intraspecific variability in foraging behavior has been a major focus for ecologists because of recognition that such variation is both widespread and ecologically important (Bolnick et al 2003; Araújo et al 2011; Ceia and Ramos 2015), even for seemingly generalist species (Araújo et al 2010; Tinker et al 2012; Cantor et al 2013; Rosenblatt et al 2015; Kernaléguen et al 2016). There has been a strong focus on resource availability and competition in explaining individual variation in foraging behavior, but variation in morphology, physiology, cognitive ability, and personality may also affect foraging behavior (Svanbäck and Bolnick 2007; Tinker et al 2008;

Araújo et al 2011; Bergvall et al 2011). Hence, quantifying consistent individual differences in foraging behavior is also of management interest because behavioral consistency may affect the ability of individuals and populations to adapt to environmental changes and as a result contribute to the persistence of populations.

Marine mammals and seabirds are long-lived marine predators that play important roles in marine and terrestrial ecosystems world-wide, largely as a result of their body size, abundance and relatively high trophic position (Bowen 1997; Morissette et al 2006; Kiszka et al 2015). Despite the dynamic nature of marine environments, individual variation in dive behavior, movement metrics, and diet in these species is not only common but often consistent through time, even among individuals in the same demographic group (Estes et al 2003; Chilvers 2008; Ceia and Ramos 2015; Orben et al 2015; Rossman et al 2015; Wakefield et al 2015). For example, individual foraging site fidelity is widespread among central-place foragers, with individuals returning to the same foraging grounds within and across years (Bradshaw et al. 2004; Arthur et al. 2015; Baylis et al. 2015; Wakefield et al. 2015). In general, individuals with similar habitat use, foraging sites, or diets often exhibit similar dive patterns (Staniland et al 2004; Tinker et al 2008; Elliott et al 2008; Woo et al 2008; Kuhn et al 2014); however, several recent studies on seabirds have found that consistency in dive behaviors is often weaker than foraging site fidelity, and that consistency in dive behavior is not always a consequence (or cause) of consistency in other foraging behaviors (Ratcliffe et al 2013; Harris et al 2014; Patrick et al 2014; Wakefield et al 2015).

California sea lions are an abundant generalist pinniped that inhabit coastal and offshore environments of the California Current System (CCS), foraging on a diversity of schooling and demersal fish and cephalopod species (Melin et al 2008; Orr et al 2011; Kuhn and Costa 2014). The abundance and distribution of prey species within the CCS, a productive eastern boundary current system, varies seasonally and annually in response to fine- and broad-scale oceanographic processes (Koslow et al 2014; Ralston et al 2014; Koslow and Davison 2015). In response, the diet of California sea lions also varies temporally, with sea lions preying on seasonally abundant aggregating species, including northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), and market squid (*Doryteuthis opalescens*; Weise and Harvey 2008). California sea lions exhibit considerable flexibility in their diving behavior and movements, using multiple foraging strategies to find epipelagic, mesopelagic, and benthic prey (Weise et al 2010; Villegas-Amtmann et al 2011). Studies on intraspecific variation in foraging behavior of California sea lions have focused primarily on describing how individuals differ, and have not explored whether behavioral differences persist through time.

California sea lions are a good model species for examining behavioral consistency in marine mammals because they are a generalist species that experiences considerable fluctuations in prey distribution and availability. The goals of this study were therefore to determine whether California sea lions exhibit consistency in foraging behaviors, and identify the factors that may drive behavioral consistency in this species. We focused on the foraging behavior of adult females, which are central-place foragers during the 10 to 11 month lactation period, alternating foraging trips to sea with time ashore nursing their pup (Melin et al 2000). Because behavioral consistency is affected by the timescale across which measurements are collected (Novak and Tinker 2015), we examined consistency in foraging behaviors at multiple temporal scales. Foraging behavior was quantified using data collected from bio-logging devices that represented fine-scale behavior at short temporal scales (days to months) and stable isotopes of carbon (C) and nitrogen (N) in whisker samples that represented broad-scale foraging behavior at a longer temporal scale (years). Specifically, we calculated how repeatable female sea lions were in their dive behavior, movements, and stable isotope values, and whether repeatability of fine-scale behaviors was affected by the number of observations per sea lion (foraging trips). We also calculated repeatability of each behavior for each sea lion to (1) determine if some individuals were more predictable than others in both fine- and broad-scale behaviors, and (2) identify the potential factors driving individual differences in repeatability of dive behavior, including foraging site fidelity, environmental consistency, and mass.

4.3. Methods

Adult female California sea lions were captured in November of 2005 to 2008 at San Nicolas Island (32.2° N, 119.5° W) using custom hoop nets. San Nicolas Island is one of the two largest California sea lion rookeries, with upwards of 20,000 pups born each year (Lowry and Maravilla-Chavez 2005). Once captured, females were sedated with gas anesthesia using a portable field vaporizer. Satellite tags, time-depth recorders, and a VHF tag were attached to the dorsal midline of each animal using a quick setting epoxy. Time-depth recorders were programmed to collect depth and temperature data at 1, 2, or 4 s intervals (depending on the year). Tags were mounted on a neoprene base and attached to mesh netting with zip-ties. Standard length and mass were also measured at initial capture. Sea lions were released and subsequently recaptured after approximately two months to recover instruments and archived data.

Whiskers were collected from 10 adult females captured at San Nicolas Island in November of 2014 (see Chapter 3). A single whisker (typically one of the longest) was plucked from the whisker bed while the sea lion was under gas anesthesia. Whisker samples were stored in paper envelopes at room temperature until analysis.

Dive and movement behavior

Location data were processed with a speed and angle filter to remove erroneous locations. Hourly at-sea locations were interpolated using either a correlated random walk (R package, *crawl*) or linear interpolation, depending on the quality of the location data (ARGOS or GPS; see Chapter 1). Dive data were subsampled to 4 s intervals to standardize across years, and processed using a custom Matlab program (IKNOS, Y. Tremblay) to obtain summary statistics for each dive (e.g., dive depth, duration). These summary statistics also included environmental data associated with each dive (temperature at surface (SST) and thermocline depth). California sea lions exhibit periods of intensive diving while at sea (diving bouts), which can be associated with either transit or foraging behavior. We used a custom-written R code (R. Beltran) to identify these bouts and exclude potential transiting dives. Bouts were excluded from analysis if the mean dive depth of the bout was less than 8 m to exclude potential transiting dives (Melin et al 2008).

The location and dive data were used to calculate 22 variables that described the dive and movement behavior of sea lions on each foraging trip to sea. A foraging trip to sea was defined as any trip to and from the rookery that lasted a minimum of one day. This criterion was chosen to exclude trips that did not span more than one time of day (day and night), which would have resulted in missing values for some of the variables. Many of these short trips were close to the rookery that typically did not have many satellite locations associated with them, and occurred infrequently for most sea lions. The duration of each foraging trip and the amount of time spent hauled-out following a trip was identified using the wet-dry sensor on the time-depth recorder. The solar zenith at departure and arrival were used as proxies for the arrival and departure time. This metric was chosen, instead of simply using the actual hour of departure or arrival, because day length changes throughout the year (e.g., the amount of available light at 18:00 is not the same in November vs. January). Location data were used to determine the maximum (farthest straight-line distance) and total distance travelled from the rookery.

Dive variables were assigned to one of two categories - dive behavior that described the characteristics of a sea lion’s foraging behavior, and dive effort that described the effort expended by sea lions while on a foraging trip (hereafter referred to as effort). Measures of dive behavior were calculated by averaging all dives across a foraging trip and included the maximum day and night dive depths (m) and durations (s), bottom time (s), the percentage of time spent diving during the day and night, the percentage of dives that were epipelagic (< 200 m), mesopelagic (> 200 m), or benthic (at or close to the bottom), and a diel index. Dive types (epipelagic, mesopelagic, or benthic) and the diel index were calculated as described in Chapter 1. Measures of effort included the percentage of time at sea spent diving, mean bout dive rate (dives hr^{-1}), mean interbout interval (h), mean bout duration (h), and mean number of bouts per day.

Isotope analysis of whiskers

Stable isotope analysis of whiskers has emerged as a powerful tool to quantify the long-term foraging behavior of pinnipeds. This method relies on the concept that stable isotopes, namely C and N, are transferred through food webs in a predictable pattern as a result of biochemical processes. Variation in the ratio of $^{13}C/^{12}C$ ratios ($\delta^{13}C$) is typically used as an indicator of foraging habitat, whereas $^{15}N/^{14}N$ ($\delta^{15}N$) typically reflects changes in trophic level (Newsome et al 2010). For California sea lions, variation in $\delta^{13}C$ values is mainly a result of how far sea lions forage from the mainland coast (higher values closer to the mainland), whereas variation in $\delta^{15}N$ is driven by diving behavior (higher values in deeper-diving sea lions; see Chapter 3). Because whiskers are metabolically inert, isotope values remained unchanged once the tissue is grown, and these archival tissues can be serially sampled to examine longitudinal patterns of isotope ratios for an individual animal. In comparison to the fine-scale data collected by bio-logging devices, isotope values in whiskers represent broad-scale behavioral patterns because slow whisker growth rates result in the integration of foraging behavior across a longer period of time.

Whiskers were sonicated for 15 minutes in de-ionized water and rinsed with petroleum ether to remove any exogenous debris. The total length of whiskers was measured before sectioning each whisker into ~3 mm segments. Tissue samples were weighed into tin boats (0.5 ± 0.05 mg) and analyzed for C and N stable isotopes using a Carlo-Erba NE2500 CHNS-O Analyzer coupled to a Thermo Finnigan DELTAplus XP Isotope Ratio Mass Spectrometer via a Thermo Finnigan ConFlo III at the University of California Santa Cruz Stable Isotope Laboratory. Results are presented in delta (δ) notation in per mil (‰) relative to either Vienna-Pee Belemnite Limestone (C) or atmospheric N_2 (N). Precision of an internal laboratory standard was 0.05 ‰ for δ^{13}C and 0.07 ‰ for δ^{15}N. Whisker growth rates were estimated as described in Chapter 3, and used to determine the amount of foraging time integrated into each segment and the entire whisker.

Population-level behavioral consistency

The repeatability of each behavioral variable (*R)* was calculated using the following equation

$$R = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$$

where σ_α^2 is the between individual variability and σ_ε^2 is the residual error (within individual variability; Dingemanse and Dochtermann 2013). Linear mixed effects models were used to quantify the between and within individual variability in each behavioral trait (Nakagawa and Schielzeth 2010; R package *lme4*). Separate models were run for each behavioral variable, with year as a fixed factor and individual as a random effect. Because we included an additional fixed effect in the analysis (year), the resulting repeatability estimates are considered adjusted repeatabilities (R_{adj}), representing the repeatability as if all measurements were taken at a fixed time (Nakagawa and Schielzeth 2010). The repeatability of whisker δ^{13}C and δ^{15}N values were estimated using the same approach, but instead of including time as a fixed effect, we limited our analyses to include isotope values within the 2 years prior to collection to ensure the behavior of individuals was represented by similar time periods. We used the R package *rptR* to calculate the significance of repeatability estimates using permutation tests, as well as bootstrapped 95% confidence intervals. Repeatability measurements ranged from 0 - 1, with greater repeatability as values approached one. We also assigned a qualitative measure of repeatability based on numerical values as described in Harris et al. (2013); behaviors with values from 0 - 0.25 had low repeatability, values of 0.25 - 0.5 were considered repeatable, values of 0.5 - 0.75 were moderately repeatable, and behaviors with values greater than 0.75 were considered strongly repeatable.

Short-term temporal variation in behavioral consistency was examined by calculating the repeatability of each behavior using 1) the first three foraging trips of each sea lion (~ 2 weeks, short), 2) the first six foraging trips (~1 month, intermediate), and 3) 10 foraging trips to sea (~1.5 months, long). Because sea lions varied in their number of foraging trips, we limited our estimates of repeatability for this analysis to the 16 sea lions that were tracked across at least 10 trips to sea. We used linear mixed effects models to evaluate whether the number of foraging trips influenced the repeatability of behavioral traits. The number of trips (short, intermediate, or long), the behavioral category (dive behavior, effort, and movement), and the interaction between the two were included as fixed factors, and each behavior was treated as a random effect to account for the non-independence of repeatability estimates within a behavior. The significance of the number of observations was assessed using *F*-tests and the Kenward-Roger approximation of degrees of freedom (R package *afex*). Multiple comparisons were made using Tukey's HSD tests (R package *multcomp*).

Individual-level behavioral consistency

The repeatability of individual sea lions (R') for each behavioral variable was calculated using the equation from Wakefield et al. (2015)

$$R'_i = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_i^2}$$

where σ_α^2 is the between individual variability and σ_i^2 is the residual variance for individual *i* from the mixed effects model. In addition, we calculated the individual repeatability of SST and thermocline depth as indicators of environmental consistency (see below). Because there were often large differences in mean behavioral values among individuals, we natural log transformed all dive and movement variables so that the residual variance represented a relative instead of an absolute change from each individual’s behavioral mean.

We used two approaches to examine the factors that may drive inter-individual variation in behavioral consistency. First, Pearson’s correlations were used to determine the relationships between individual repeatability of different behaviors (i.e., was an individual more likely to exhibit repeatability for behavior x if it was repeatable for behavior y), as well as between individual repeatability and the mean values of behavioral variables (i.e., do individuals with greater mean values of behavior x tend to also be more repeatable in behavior x). Bonferroni corrections were applied to adjust for multiple comparisons where applicable. Comparisons were made for both fine- and broad-scale behaviors, but because whiskers were not collected from the same sea lions used in the short-term behavioral analysis, we could not make any comparisons between short- and long-term behavioral consistency. Secondly, we used linear models to examine whether foraging site fidelity (see below), consistency in SST or thermocline depth, year, or body mass explained any of the variability in individual repeatability of dive behavior. We ran all possible combinations of models without interactions (separate models were run for each variable), and used Akaike Information Criterion corrected for small sample (AIC_c) to inform model selection. We assumed that all models within two ΔAIC_c values of the top model were equivalent to the top model.

An index of foraging site fidelity (FI) was calculated for each sea lion using a modified equation from (Willis-Norton et al 2015) where

$$FI_{ij} = | 2 \bullet \left[\left(dist_i - dist_j \right) / \max \left(dist_i , dist_j \right) \right] | + \left[\left(angle_i - angle_j \right) / 90 \right]$$

dist is the maximum straight-line distance from the rookery for trips *i* and *j*, and *angle* is the angle between the rookery and the maximum straight-line distance for trips *i* and *j* ($angle_i > angle_j$). Fidelity index values ranged from 0 - 4; two foraging trips that were similar in their overall distance and angle from the rookery had a FI value close to zero, with increasing values as trips diverged in one or both variables. Fidelity indices were calculated for each combination of trips per sea lion, and averaged to obtain one value per sea lion.

4.4. Results

A total of 32 adult female California sea lions were tracked across at least six foraging trips to sea (Table 4.1). The mean tracking duration (± SD) was 62.2 ± 12.0 days, with an average of 10 ± 3 trips per sea lion. Because of differences among individuals in trip durations, similar tracking durations were not necessarily associated with the same number of foraging trips (Table 4.1). Stable isotope values in whiskers across the 2-year period ranged from -14.4 to -16.3 ‰ for δ^{13}C values and 16.1 to 18.0 ‰ for δ^{15}N values.

Population-level behavioral consistency

Repeatability estimates for all 22 fine-scale behaviors were significant, but the strength of repeatability varied widely among behaviors ($R = 0.11 - 0.82$, $p < 0.01$). In general, dive behaviors were more repeatable than effort or movement variables

(Figure 4.1), with the exception of bout dive rate ($R = 0.72$) and the percentage of time at sea diving ($R = 0.55$). These two variables were more similar in repeatability to dive behaviors ($R = 0.41 - 0.82$) than other measures of effort ($R = 0.27 - 0.40$). Sea lions were moderately repeatable in their broad-scale foraging behavior across longer time periods (Figure 4.1), with slightly higher repeatability estimates for δ^{15}N (R =0.63, $p < 0.01$) than δ^{13}C values (R =0.52, $p < 0.01$).

Temporal variability in behavioral consistency

Repeatability estimates for dive behaviors ($F_{2,20} = 4.59$, $p = 0.02$) and effort ($F_{2,8} = 18.11$, $p = 0.02$), but not movements ($F_{2,10} = 1.63$, $p = 0.24$) were affected by the number of foraging trips sea lions were tracked across. For dive behaviors, repeatability was significantly lower during long (10 foraging trips) compared with short time periods (3 foraging trips; $p < 0.01$). For effort, repeatability was significantly lower during long and intermediate compared with short time periods ($p < 0.01$ for both short-intermediate and short-long). Out of all the variables, repeatability estimates of the percentage of benthic and epipelagic dives, and the percentage of time diving at night were the least affected by the number of foraging trips (Figure 4.2). Despite significant changes in repeatability, the magnitude of the changes was relatively small and the overall trends in repeatability among variables were similar regardless of the number of observations used to calculate repeatability.

Individual-level behavioral consistency

There was considerable variation in estimates of individual repeatability, with some individuals exhibiting strong repeatability in fine-scale behaviors that were only weakly to moderately repeatable at the population level, and vice versa. For example, there were three sea lions that exhibited moderate to strong repeatability in the solar zenith at arrival (they always arrived between 22:00 and 2:00) despite that this was a weakly repeatable behavior at the population level. Individual repeatability estimates of isotope values showed similar trends across the entire two-year period ($R'_{\delta^{13}C}$ = 0.28 - 0.75, $R'_{\delta^{15}N}$ = 0.47 - 0.92), although values of sequential whisker segments tended to clump together in isospace for all sea lions (Figure 4.3). Sea lions exhibited a range of behavior in terms of their overall consistency in diving behavior, foraging site fidelity, and stable isotope values (Table 4.2, Figures 4.3 - 4.4). For example, some sea lions exhibited moderate to strong repeatability in dive behavior and strong foraging site fidelity, whereas others exhibited strong site fidelity but were less consistent in dive behavior. Despite these individual differences, all sea lions exhibited some level of consistency when repeatability was averaged across all dive behaviors ($\overline{R}'_{dive}$ = 0.46 - 0.89). Similarly, sea lions captured in 2014 were moderately repeatable in at least one isotope across the 2-year period.

There were correlations between individual-level repeatability estimates of different fine-scale behaviors (Table 4.3), but no correlation between repeatability estimates of δ^{13}C and δ^{15}N ($r = 0.22$, $p = 0.55$). The strongest correlations in repeatability estimates for fine-scale behaviors were between variables whose mean values were also strongly correlated with each other (e.g., dive depth and duration), but there were a few variables that were notable because they were correlated with multiple variables. For example, individual repeatability in night dive depth and duration were correlated with individual repeatability of dive rate ($r = 0.68$), diel behavior ($r = 0.57$), percentage of time at sea diving ($r = 0.55$), percentage of time spent diving at night ($r = 0.66$), and the percentage of benthic dives ($r = 0.52$).

There were also correlations between individual-level repeatability and the mean value of that trait for fine-scale behaviors, but not stable isotopes $\delta^{13}C$: $r = -0.02$, $p = 0.96$, $\delta^{15}N$: $r = -0.45$, $p = 0.19$). There were positive correlations between individual repeatability and the mean trait value for the percentage of time diving during the day, the percentage of epipelagic or benthic dives, the diel index, and the solar zenith at arrival ($r = 0.71 - 0.82$). There were negative correlations between individual repeatability and the mean value for night depth ($r = -0.62$) and night duration ($r = - 0.54$), indicating that at night, females that dove deeper or for longer were less repeatable in their dive depths than shallower diving females.

Individual variability in the consistency of dive behaviors was not well explained by foraging site fidelity, environmental consistency, mass, or year. There were six variables where the intercept only was the top model or within 2 ΔAIC_c of the top model (day and night dive depth and duration, bottom time, percentage of benthic dives), with very little variability explained by any of the models ($r^2 < 0.1$). For the remaining dive behaviors, there was at least one explanatory variable that was important (Table 4.4), although the amount of variability explained was still relatively low ($r^2 \leq 0.31$). Year was important in explaining variability in individual repeatability for the percentage of time diving during the day, the percentage of epipelagic dives, and the diel index. Mass was important in explaining individual repeatability in the percentage of time spent diving at night. Foraging site fidelity was in all three top models for the percentage of time spent diving mesopelagically, and a non-informative parameter for two other variables.

4.5. Discussion

Population-level behavioral consistency

Adult female California sea lions exhibited consistency in both fine- and broad-scale foraging behaviors across multiple temporal scales. Population-level consistency in dive behavior and movements may arise in part because sea lions repeatedly forage on different prey types or prey age classes that vary in their horizontal and/or vertical distribution. This may explain the occurrence of short-term behavioral consistency, as prey availability and distribution is likely more stable within than across seasons. Despite the dynamic nature of the CCS, female sea lions still exhibited less variability in their foraging behavior across longer time scales than was present at the population level, suggesting that factors other than prey may drive behavioral consistency in this species. Behavioral variation is rarely discussed in the context of personality for pinnipeds (Twiss and Franklin 2010), but there is growing evidence from other taxonomic groups that classic personality traits affect foraging behavior and can drive individuals to use different strategies (Kurvers et al 2010; van Overveld and Matthysen 2010; Bergvall et al 2011; Patrick and Weimerskirch 2014; Mella et al 2015). These classic personality traits, such as boldness, have not been measured in pinnipeds due to logistical challenges, but warrant attention give the increasing evidence for the link between foraging behavior and personality.

The strength of behavioral consistency varied both within and among behavioral categories, with dive behaviors generally more repeatable than either effort or movement variables. This is consistent with the finding from Chapter 1 that foraging trips of female sea lions could be classified into one of three foraging strategies based on dive behaviors, and that most females used one primary strategy during the tracking duration. The higher repeatability of dive rate and the proportion of time spent diving compared with other variables of effort is likely because they tend differ widely among foraging strategies. As a result, these variables may be more repeatable because they are more indicative of foraging strategy than effort, at least when comparing across foraging strategies. The lower repeatability of other metrics of effort and trip duration for California sea lions and other central-place foragers (Soanes et al 2012; Patrick et al 2014; Baylis et al 2015; Wakefield et al 2015) suggests that these behaviors are affected by either the spatial distribution and composition of specific prey patches (e.g., density) or the foraging success of individuals.

The moderate to strong repeatability of dive behaviors exhibited by California sea lions is in contrast to studies on seabirds that have generally found diving behavior is only weakly to moderately repeatable (Cook et al 2005; Woo et al 2008; Ratcliffe et al 2013; Harris et al 2014; Patrick et al 2014; Wakefield et al 2015). Similar to pinnipeds, northern gannets (*Morus bassanus*) primarily forage on small forage fish and larger pelagic fish (Lewis et al 2003; Garthe et al 2007), making it unlikely that these differences are solely a result of prey type or behavior. The diving behavior of almost all seabirds is constrained by the evolutionary tradeoff between a body plan adapted for flight in air and diving in water, which limits their dive depth and range of available prey options. As a result, many seabirds may not exhibit strong repeatability in dive behaviors because there is less flexibility for inter-individual variation than for penguins and pinnipeds, which are more adapted for an aquatic lifestyle. Alternatively, it is possible that seabirds are less consistent in their dive behavior because they use different foraging cues (e.g., olfactory, visual, social) to find prey patches that result in a more opportunistic behavior than pinnipeds. Given the general lack of information about repeatability in dive behavior of both marine mammals and seabirds, further research is needed to ascertain whether these preliminary differences are representative of a more general trend.

Temporal variability in behavioral consistency

The consistency of fine-scale foraging behaviors generally decreased as sea lions were tracked across longer time periods. Although we did not test for a similar trend in the isotope data, the tendency for sequential whisker segments to group closely in isospace is suggestive of a similar pattern across a much longer temporal scale (months to years). The change in behavioral consistency between short (3 foraging trips), intermediate (6 foraging trips), and long-time periods (10 foraging trips) was greatest for bout duration, bout interval, and the number of bouts per day, which is consistent with the idea that these variables are reflective of the characteristics of prey patches. Bathymetric and oceanographic features may concentrate prey in predictable areas at coarse scales (Polovina et al 2001; Bost et al 2009), but the persistence of individual prey patches within these regions may only last for a few weeks (Davoren et al 2003). For sea lions, the duration of three foraging trips was ~ 2- 3 weeks, providing some evidence that the high behavioral consistency across short time periods likely occurs because they forage within the same patch. Sea lions may use memory to return to the same patch across short time periods, as has been suggested for other central-place foragers (Bonadonna et al 2001; Davoren et al 2003; Regular et al 2013), only moving to a new patch when the current patch is no longer profitable or has dispersed. The similarity in behavioral consistency between intermediate (6 foraging trips) and longer time periods (10 foraging trips) may be because the general characteristics of patches are likely similar within a season; as a result, intra-individual variation in behavior does not drastically change once the number of visited foraging patches exceeds one. There were three variables that did not appear to be affected by the number of foraging trips: percentage of epipelagic and benthic dives, and the percentage of time spent diving at night. This lack of change is likely because these variables, particularly those related to dive type (epipelagic or benthic), are reflective of the type of prey in the environment, which may be more static across several months.

Individual-level behavioral consistency

Sea lions varied in their level of behavioral consistency, with some individuals exhibiting greater predictability in their behavior than others. This trend was irrespective of the time scale across which measurements were collected, as the whisker isotope data revealed similar patterns. The presence of inter-individual differences in predictability is consistent with several recent studies that have shown that even generalist species are often comprised of generalist and specialist individuals (Araújo et al 2010; Tinker et al 2012; Cantor et al 2013; Kernaléguen et al 2016). Despite this, almost all sea lions were at least moderately repeatable in their overall dive behavior and at least one isotope, suggesting that sea lions exhibit considerably less variability in their foraging behavior than present at the population level across short- and long time periods.

Similar to the findings of Wakefield et al (2015), individual foraging site fidelity did not appear to be the cause (or consequence) of consistency in dive behavior. The exception to this was for individual repeatability in the percentage of mesopelagic dives, which is likely because deep-diving appears to be a spatially explicit strategy, at least for sea lions from San Nicolas Island (see Chapter 1). This would also explain the relationship between individual repeatability in the percentage of mesopelagic dives and SST, as females that forage in the same spot are likely to experience consistent environmental conditions. Body size was also not important in explaining individual consistency, with the exception that smaller females tended to be more consistent in the percentage of time spent diving at night. Given that deep-diving at night was associated with less consistency in other night-time diving behaviors, this ultimately may have been a result of physiological constraints on dive depth (i.e., very small females tend not to exhibit frequent deep dives). Alternatively, it is possible that some of these small females were relatively young and therefore pursued more ‘common’ foraging strategies because they did not have the experience or knowledge of alternative prey types.

We could not test for the relationship between individual consistency in dive behavior and diet, but several factors suggest that prey type is a driving factor for at least some behaviors. First, year explained a significant amount of variability in individual repeatability of three behaviors that are likely linked to the abundance of schooling fish in the environment. Northern anchovy and sardine, which are both important epipelagic prey items for female sea lions (Orr et al 2011; Melin et al 2012), form schools at depth during the day that disperse when they migrate to shallower waters at night (Kaltenberg and Benoit-Bird 2009). Their abundance varies annually (Koslow and Davison 2015), which may explain why individual repeatability in the percentage of time spent diving during the day, percentage of epipelagic dives, and diel behavior varies among years. Secondly, deeper diving females were not only less consistent in their night dive depth, but individual repeatability in night dive depth was positively correlated with repeatability of the percentage of time diving at night, dive rate, and the diel index. This suggests that females that forage deeper in the water column at night may forage on multiple prey species or on species that are less predictable in their behavior, making them less consistent in their dive behavior than sea lions that forage on species that predictably migrate to the surface at night.

Conclusion

California sea lions exhibited behavioral consistency at the population- level across both short- and long temporal scales, although the strength of this consistency varied among behaviors. Sea lions also varied in the strength of behavioral consistency at the individual-level, but individual consistency in dive behavior was largely independent of foraging site fidelity. Prey type is a likely driver of behavioral consistency at both the population- and individual-level, although it remains unknown what factors actually drive individual sea lions to choose different prey types. The decreasing strength of behavioral consistency with time suggests that sea lions do alter their behavior in response to environmental changes, although most sea lions exhibited considerably less behavioral variation than was present at the population level. This was true despite the occurrence of several periods of poor food availability and reproductive success between 2012 and 2014, the time period represented by the isotope data, indicating that most sea lions may “stick to what they know” even in the face of environmental changes. While this may be a successful strategy for survival, it raises questions about how the strategies that individual animals use to cope with environmental variability affect reproductive fitness. These questions remain largely unanswered for marine mammals, but are of both ecological and evolutionary importance given the widespread environmental changes occurring in marine ecosystems worldwide.

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Table 4.1. Summary statistics for each sea lion, including the tracking duration, number of trips, standard length, and mass. The third and fourth numbers in each ID correspond to the year (2005 - 2008) of instrumentation.

Sea lion ID	Duration (days)	# Trips	Length (cm)	Mass (kg)
2105029	59.2	15	166	69.4
2105030	51.2	9	171	86.4
2105031	54.3	8	158	73.6
2105032	26.5	6	159	86.2
2105033	56.7	13	161	91.4
2105034	61.9	12	167	96.0
2105035	56.7	15	165	93.6
2105036	39.1	6	154	78.6
2105037	51.3	12	166	90.0
2105038	60.1	9	150	63.6
2105039	48.9	10	-	-
2106001	62.6	8	172	85.8
2106002	62.2	10	167	79.2
2106003	67.2	6	157	66.0
2106004	61.5	7	160	77.4
2106005	63.6	7	155	62.2
2106007	64.4	9	161	76.0
2106009	60.5	7	169	87.4
2107009	81.4	12	164	91.2
2107010	73.6	12	165	83.2
2107011	71.7	16	167	91.2
2107012	75.0	8	173	95.4
2107013	76.8	11	156	77.8
2107014	72.9	16	163	83.4
2107015	79.0	18	169	95.6
2107016	79.6	9	166	80.2
2107017	73.4	14	172	83.6
2108001	60.0	13	169	95.4
2108002	66.5	9	165	85.4
2108005	66.6	7	155	97.2
2108006	57.1	8	166	84.6
2108010	48.5	12	161	86.4

Table 4.2. Repeatability estimates across foraging trips for individual female California sea lions in each dive behavior. The mean repeatability of each individual (Mean) and foraging site fidelity (FI) are also shown. Larger values of repeatability indicate that a behavior/individual was more repeatable, whereas larger values for FI indicate lower site fidelity.

Sea lion ID	% Time Diving		Dive Depth		Dive Duration		% Dive Type			Bottom time	Diel	Mean	FI
	Day	Night	Day	Night	Day	Night	Epi	Benthic	Meso				
2105029	0.81	0.87	0.88	0.82	0.83	0.70	0.97	0.91	0.99	0.65	0.51	0.81	0.82
2105030	0.86	0.86	0.89	0.91	0.89	0.86	0.95	0.91	0.97	0.83	0.86	0.89	1.43
2105031	0.78	0.86	0.93	0.93	0.94	0.83	0.81	0.74	0.96	0.74	0.63	0.83	0.89
2105032	0.11	0.68	0.48	0.68	0.38	0.62	0.91	0.72	0.69	0.49	0.27	0.55	0.83
2105033	0.55	0.21	0.86	0.69	0.89	0.81	0.96	0.71	0.95	0.69	0.88	0.75	0.31
2105034	0.77	0.22	0.89	0.48	0.80	0.32	0.56	0.82	0.93	0.57	0.33	0.61	0.24
2105035	0.58	0.78	0.79	0.88	0.76	0.86	0.99	0.53	0.76	0.87	0.62	0.77	0.76
2105036	0.79	0.81	0.98	0.89	0.91	0.90	0.82	0.88	1.00	0.84	0.74	0.87	0.27
2105037	0.29	0.15	0.67	0.41	0.62	0.34	0.39	0.45	0.95	0.68	0.10	0.46	1.02
2105038	0.48	0.72	0.61	0.83	0.55	0.65	0.61	0.73	0.63	0.49	0.62	0.63	0.73
2105039	0.44	0.89	0.59	0.96	0.68	0.87	0.72	0.59	0.76	0.85	0.14	0.68	0.39
2106001	0.86	0.61	0.82	0.82	0.79	0.53	0.40	0.70	0.72	0.43	0.96	0.69	0.80
2106002	0.74	0.86	0.56	0.32	0.56	0.28	0.56	0.56	0.43	0.74	0.44	0.55	0.62
2106003	0.58	0.52	0.89	0.93	0.90	0.87	0.88	0.88	0.92	0.73	0.97	0.82	1.07
2106004	0.37	0.84	0.95	0.87	0.96	0.84	0.69	0.90	0.89	0.81	0.91	0.82	0.39
2106005	0.82	0.88	0.84	0.92	0.77	0.87	0.68	0.97	0.94	0.74	0.96	0.85	0.48
2106007	0.90	0.84	0.85	0.97	0.73	0.72	0.85	0.67	1.00	0.68	0.76	0.82	0.11
2106009	0.97	0.85	0.95	0.95	0.91	0.73	0.72	0.94	0.99	0.75	0.99	0.89	0.40

Sea lion ID	% Time Diving		Dive Depth		Dive Duration		% Dive Type			Bottom time	Diel	Mean	FI
	Day	Night	Day	Night	Day	Night	Epi	Benthic	Meso				
2107009	0.68	0.61	0.61	0.94	0.51	0.94	0.84	0.78	0.93	0.67	0.80	0.75	0.12
2107010	0.45	0.73	0.83	0.89	0.86	0.86	0.88	0.47	0.84	0.45	0.52	0.71	0.32
2107011	0.63	0.18	0.91	0.58	0.86	0.45	0.86	0.62	0.77	0.56	0.34	0.61	0.23
2107012	0.64	0.85	0.80	0.87	0.82	0.79	0.62	0.74	0.92	0.69	0.67	0.76	1.12
2107013	0.36	0.42	0.82	0.88	0.92	0.79	0.66	0.91	0.97	0.73	0.50	0.72	0.62
2107014	0.42	0.56	0.77	0.63	0.70	0.51	0.80	0.60	0.64	0.47	0.48	0.60	1.14
2107015	0.17	0.14	0.87	0.44	0.80	0.33	0.62	0.62	0.98	0.79	0.29	0.55	0.26
2107016	0.12	0.41	0.73	0.47	0.89	0.44	0.44	0.66	0.68	0.78	0.36	0.54	1.16
2107017	0.28	0.30	0.85	0.44	0.73	0.42	0.77	0.52	0.91	0.61	0.19	0.55	0.67
2108001	0.75	0.33	0.93	0.81	0.90	0.74	0.73	0.60	0.93	0.74	0.72	0.74	0.34
2108002	0.16	0.88	0.58	0.86	0.61	0.75	0.41	0.83	0.95	0.71	0.30	0.64	0.27
2108005	0.55	0.71	0.92	0.84	0.90	0.65	0.58	0.86	0.87	0.71	0.95	0.78	0.41
2108006	0.49	0.86	0.55	0.89	0.33	0.72	0.22	0.68	0.95	0.27	0.20	0.56	0.90
2108010	0.20	0.77	0.69	0.98	0.75	0.88	0.35	0.95	0.59	0.72	0.79	0.70	1.32

Table 4.3. Correlations between individual repeatability estimates for behavioral traits. Only variables that were moderately correlated (*r* ≥ 0.5) are shown.

Behavior	*r*
Night Duration & Night Depth	0.91
Total Distance & Max Distance	0.91
Day Duration & Day Depth	0.89
Trip Duration &Total Distance	0.85
Bout Interval & # Bouts per Day	0.82
Trip Duration & Max Distance	0.73
Night Duration & Dive Rate	0.69
Night Depth & Dive Rate	0.68
Night Depth & % Night Dive	0.66
Max Distance & Bout Interval	0.63
% Dive & % Benthic	0.62
Trip Duration & Bout Interval	0.62
Total Distance & Bout Interval	0.60
Bout Interval & Bout Duration	0.59
Bout Duration & # Bouts per Day	0.59
Diel & % Benthic	0.59
Night Depth & Diel	0.57
Night Duration & % Night Dive	0.57
Bout Duration & % Dive	0.56
Diel & % Day Dive	0.56
Night Depth & % Dive	0.55
% Dive & # Bouts per Day	0.54
Night Duration & Diel	0.54
Night Depth & % Benthic	0.52
Dive Rate & % Mesopelagic	0.52
Day Depth & % Mesopelagic	0.52
Day Duration & Bottom Time	0.52
Depart Zenith & Arrive Zenith	0.51
Diel & Day Depth	0.51
Dive Rate & % Benthic	0.51
% Benthic & # Bouts per Day	0.50

Table 4.4. Model output for the five dive behaviors where the intercept-only model was not one of the top models. For each behavior, model parameters are shown for all models within 2 ΔAIC_c of the top model. The intercept-only model is shown for comparison. Adjusted r^2 values are presented when the model contained more than one variable.

Behavior	k	logLik	AIC_c	ΔAIC_c	w	r^2
Diel						
Year	5	2.61	7.19	0.00	0.31	0.30
Intercept-only	2	-2.88	10.18	2.99	0.07	0.00
% Day Dive						
Year	5	3.99	4.43	0.00	0.23	0.28
Year + FI	6	4.75	5.99	1.57	0.11	0.20
Intercept-only	2	-1.02	6.46	2.04	0.08	0.00
% Night Dive						
Mass	3	1.20	4.49	0.00	0.28	0.16
Intercept-only	2	-1.57	7.56	3.07	0.06	0.00
% Epipelagic						
Year	5	11.34	-10.28	0.00	0.24	0.31
Year + FI	6	12.51	-9.52	0.76	0.16	0.26
Intercept-only	2	5.59	-6.75	3.53	0.04	0.00
% Mesopelagic						
FI + SST	4	19.86	-30.17	0.00	0.26	0.16
FI	3	17.86	-28.83	1.34	0.13	0.11
FI + Thermocline	4	19.11	-26.68	1.50	0.12	0.12
Intercept-only	2	16.06	-27.69	2.48	0.07	0.00

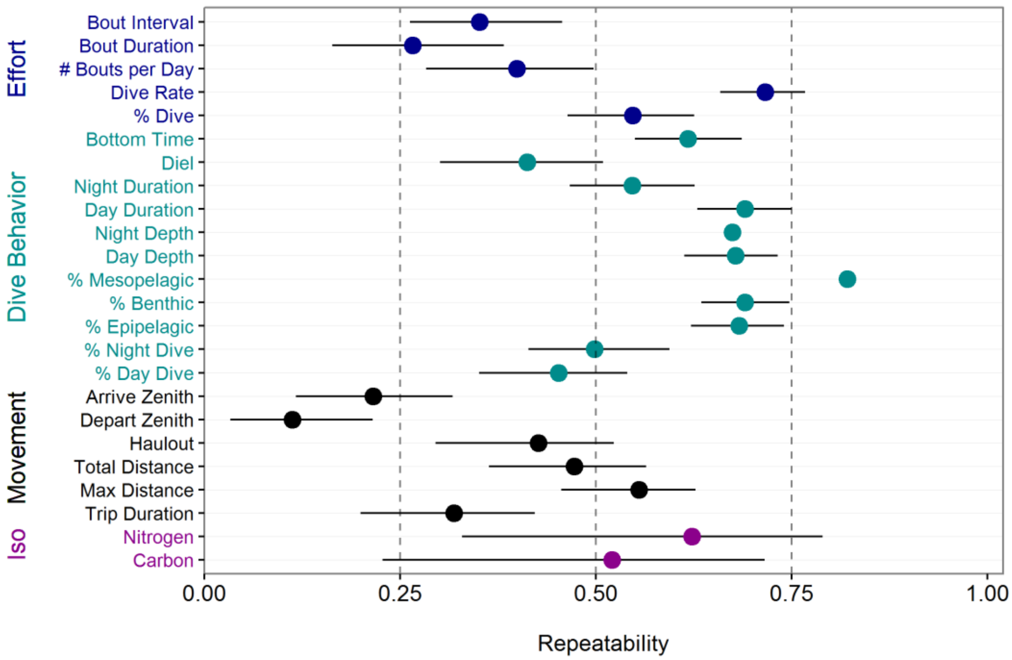

Figure 4.1. Repeatability estimates of behavioral traits of adult female California sea lions with 95% CI. Behaviors are color-coded by category (effort, dive behavior, movement, isotopes), with the first three categories representing short-term consistency (2 months; *n* = 32 sea lions) and the final category representing long-term consistency (2 years; *n* = 10 sea lions). Confidence intervals are not presented for Night Depth and % Mesopelagic because these variables were log-transformed. Cutoffs values for qualitative assessments of the strength of repeatability are shown with dashed gray lines.

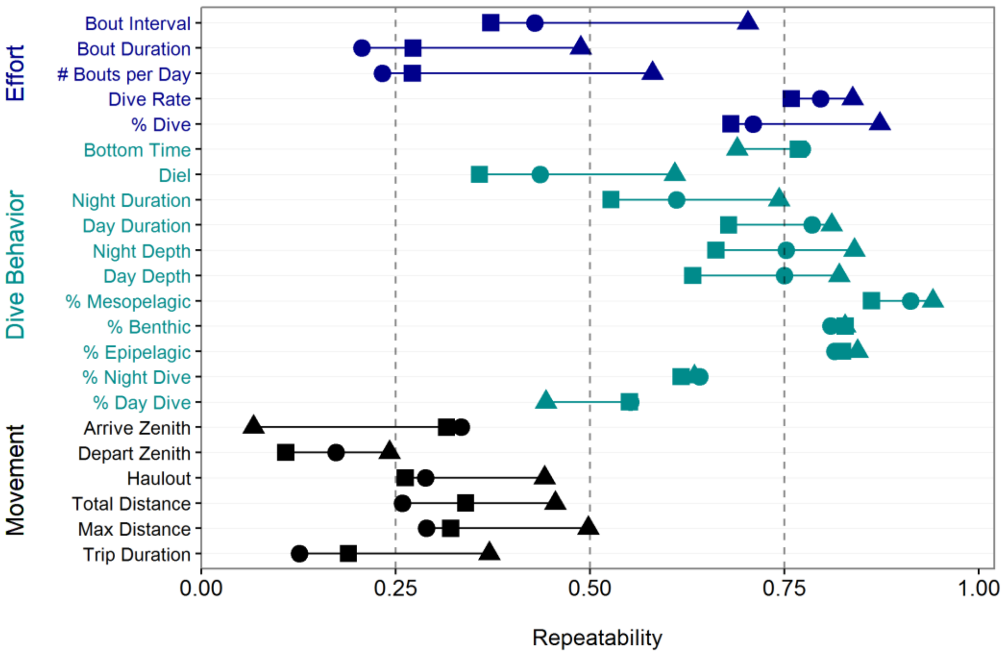

Figure 4.2. Repeatability estimates of behavioral traits for 16 adult female California sea lions using three (triangle), six (circle), and ten (square) foraging trips to sea. Cutoffs values for qualitative assessments of the strength of repeatability are shown with dashed gray lines.

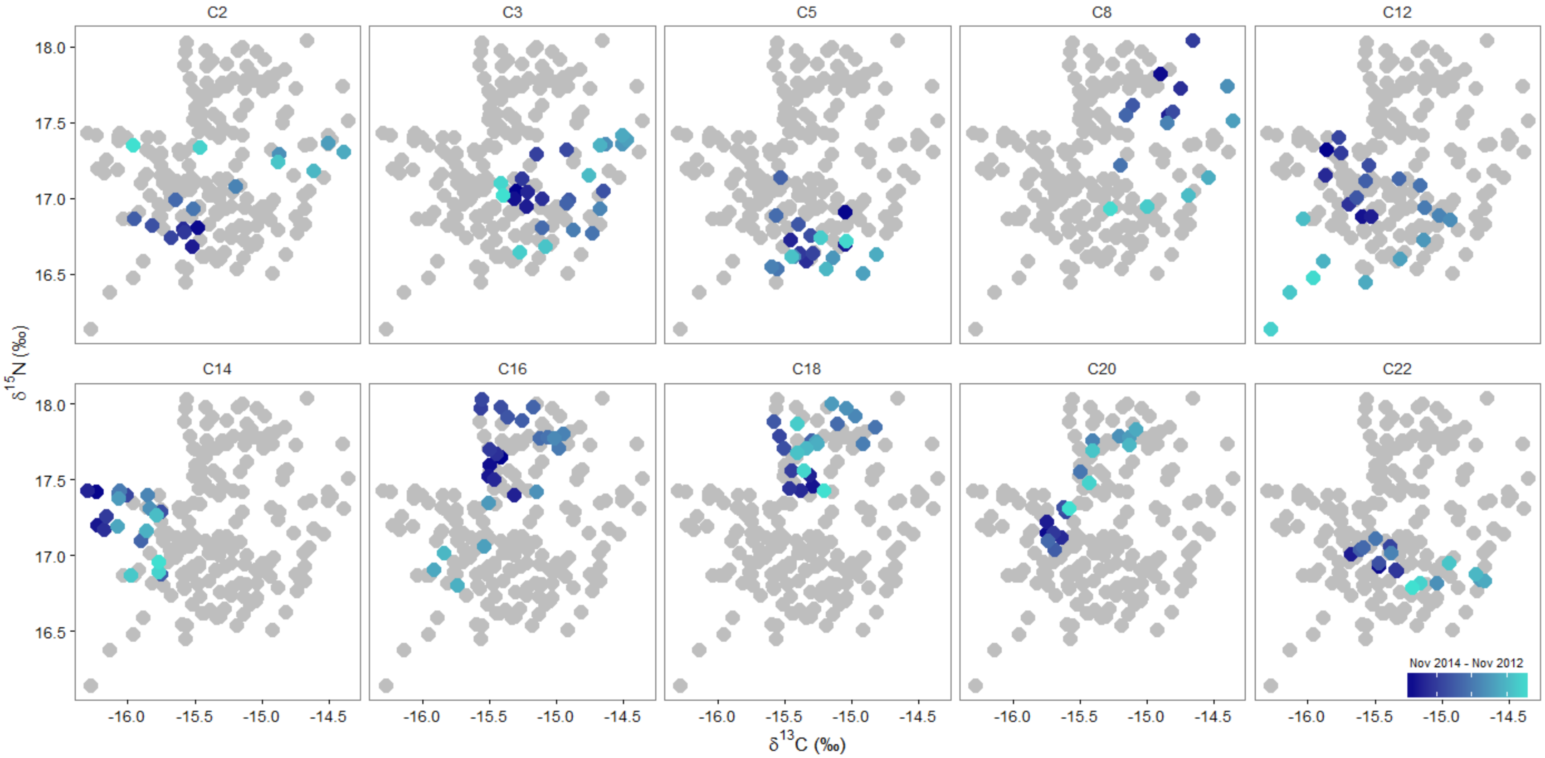

Figure 4.3. Isotope values of δ^{15}N and δ^{13}C in sequential whisker segments of adult female California sea lions. Each subplot represents a different individual, with darker colors indicative of more recent growth. The position of all sea lions in isospace is depicted by gray circles in each subplot.

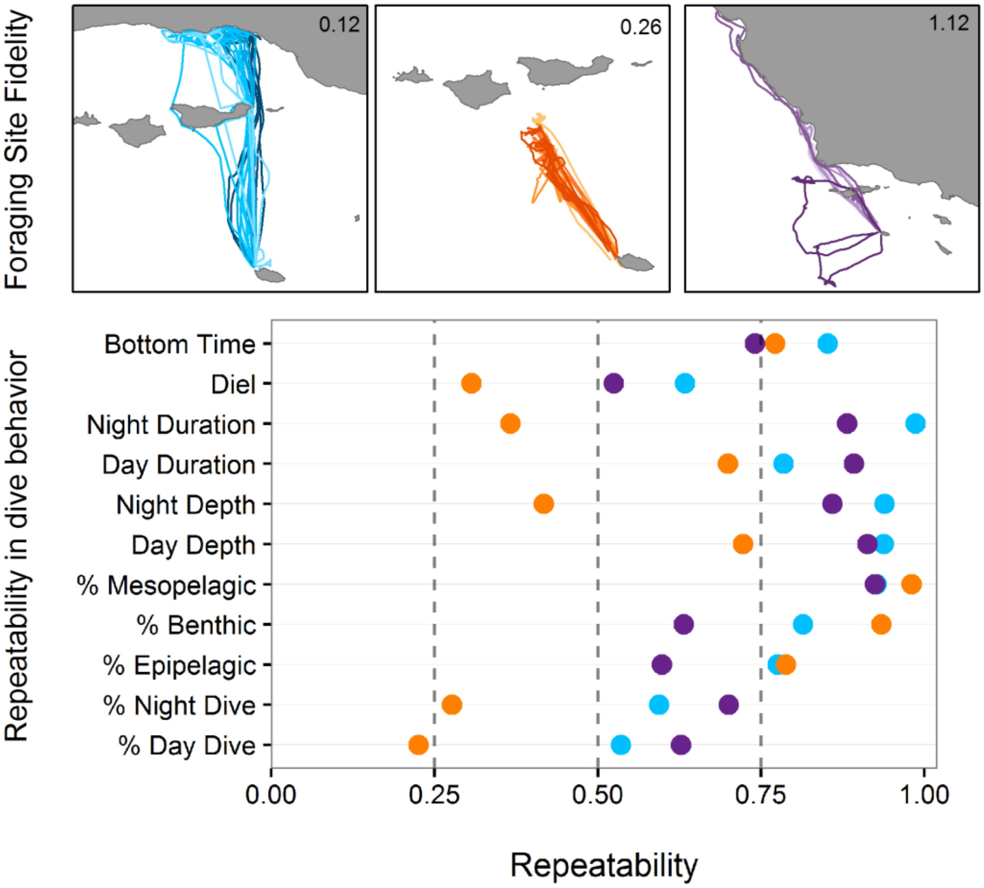

Figure 4.4. Plots from three representative individuals showing the relationship between foraging site fidelity and individual repeatability in dive behavior. In the top panel, darker colors represent foraging trips that occurred at the beginning of the tracking duration. The foraging index value is shown in the upper right hand corner, with lower values indicative of stronger site fidelity. In the lower panel, values closer to one represent higher repeatability. Each top panel represents one of three scenarios: high foraging site fidelity and high behavioral repeatability (blue), high foraging site fidelity but lower behavioral repeatability (orange), and low foraging site fidelity but high behavioral repeatability (purple).

SYNTHESIS

California sea lions are generally considered to be epipelagic foragers, but it is clear that they exhibit a much greater diversity of foraging behaviors than most otariids. This diversity has likely allowed them to be successful in such a dynamic ecosystem, as there is evidence that female sea lions switched foraging strategies in response to changes in the availability of prey (Chapter 1). Despite this apparent flexibility, female sea lions generally exhibited behavioral consistency across both short and long time scales, including periods of reduced prey availability (Chapter 4). These conclusions may at first appear at odds with each other, but consistency in isotope values is only a proxy for behavior, and there were no differences in stable isotope values between the epipelagic and mixed benthic foraging strategies. Collectively, these results indicate that female California sea lions likely do switch foraging strategies, but it is unlikely that most sea lions routinely use all three strategies. Instead, they largely appear to play it safe by consistently using similar habitats and/or dive behaviors, which may be a successful strategy for managing uncertainty in environmental conditions. These individual behavioral differences have implications for survival and reproductive fitness, as fine-scale behavior does affect energy expenditure, but not in the same way for sea lions using different foraging strategies (Chapter 2). Energy differences may have a large impact on some sea lions when they are unable to obtain sufficient energy using familiar foraging behaviors, particularly as it relates to reproductive success.

The California Current System has recently shifted towards a period of increased SST and reduced primary productivity, which has resulted in several years of poor reproductive success for California sea lions (Leising et al. 2015). Although these periods of reduced primary productivity are not new in the recent history of this species (Bograd and Lynn 2003), the effects of current conditions may be compounded by a large population size and competition from commercial fisheries. The focus of my dissertation, behavioral variability and the relationship between behavioral changes and energy expenditure, are two key components in understanding individual- and population-level changes of California sea lions to recent and future oceanographic shifts. In addition, results from my dissertation raise some interesting evolutionary questions if these oceanographic conditions persist across evolutionary-relevant time periods, particularly as it relates to opposing selective pressures of reduced food availability and behavioral flexibility on body size.

APPENDICES

A.1. Whisker growth rates estimated from linear regressions between whisker length and time for five California sea lions (Ronan, Rio, Nemo, Sake, Cali). Values are only shown for whiskers that exhibited significant positive growth ($p \leq 0.05$). Whisker labels correspond to side of the bed (R or L), the row (A - F), and the column within the row. The minimum whisker lifespan (age) was estimated for whiskers with $r^2 > 0.5$ by dividing the maximum measured length of the whisker by the growth rate. Bolded values represent lengths and estimated lifespans calculated from the new growth of lost whiskers.

Whisker	Growth rate (mm day^{-1})	r^2	Max length (cm)	Whisker lifespan (years)
Ronan				
RD1	0.045	0.50	9.7	5.9
RE1	0.052	0.36	12.2	NA
RF1	0.041	0.74	8.1	5.4
RB2	0.004	0.26	2.4	NA
RC2	0.008	0.14	4.8	NA
RD2	0.060	0.71	9.4	4.3
RE2	0.063	0.74	9.6	4.2
RB3	0.007	0.35	2.4	NA
RD3	0.017	0.26	6.8	NA
RE3	0.031	0.42	7.3	NA
RF3	0.012	0.44	3.1	NA
RC4	0.012	0.32	3.7	NA
RD4	0.013	0.36	4.6	NA
RE4	0.007	0.20	4.1	NA
RB5	0.002	0.15	1.9	NA
RC6	0.015	0.77	2.4	4.6
RD6	0.010	0.38	2.7	NA
RE6	0.007	0.16	2.2	NA
RD7	0.005	0.20	2.2	NA
LC1	0.008	0.21	3.9	NA
LD1	0.016	0.20	8.6	NA
LE1	0.019	0.20	9.5	NA
LF1	0.033	0.67	8.0	6.6
LA2	0.016	0.76	**0.7**	**1.3**
LE2	0.014	0.19	7.9	NA
LB3	0.010	0.58	2.3	6.5
LC3	0.008	0.26	3.8	NA
LB4	0.007	0.45	2.1	NA
LC4	0.007	0.19	3.3	NA
LD4	0.006	0.24	4.1	NA
LE4	0.008	0.32	3.8	NA
LE5	0.007	0.24	2.9	NA
LC6	0.009	0.62	2.1	6.5
LD6	0.006	0.20	2.7	NA
LE6	0.004	0.29	1.9	NA

Whisker	Growth rate (mm day^{-1})	r^2	Max length (cm)	Whisker lifespan (years)
LD7	0.006	0.15	1.7	NA
Rio				
RC1	0.011	0.33	4.5	NA
RF1	0.022	0.37	4.9	NA
RC2	0.011	0.71	4.2	10.7
RF2	0.081	0.85	4.7	1.6
RC3	0.010	0.58	3.3	8.7
RD3	0.007	0.14	4.9	NA
RD5	0.006	0.16	2.8	NA
RD7	0.005	0.31	2.1	NA
LB1	0.007	0.22	2.6	NA
LC1	0.025	0.83	5.1	5.6
LD1	0.009	0.12	6.9	NA
LE1	0.031	0.76	4.3*	3.7*
LF1	0.037	0.80	5.7	4.2
LC2	0.018	0.85	4.7	7.3
LD2	0.026	0.60	6.4	6.8
LE2	0.015	0.25	6.1	NA
LF2	0.012	0.22	4.1	NA
LB3	0.030	0.66	2.1*	1.9*
LC3	0.011	0.63	4.0	10.3
LC4	0.007	0.20	3.7	NA
LC6	0.003	0.19	2.0	NA
LC7	0.024	0.79	1.1	1.3
Sake				
RA1	0.038	0.96	3.1	2.2
RB1	0.014	0.19	4.5	NA
RC1	0.035	0.48	12.2	NA
RE1	0.085	0.48	17.8	NA
RA2	0.014	0.69	2.1	4.0
RC2	0.106	0.96	7.0	1.8
RD2	0.067	0.53	15.0	6.1
RE2	0.099	0.74	16.1	4.5
RA3	0.008	0.49	2.3	NA
RB3	0.011	0.65	4.3	10.6
RC3	0.042	0.94	4.6	3.0
RF3	0.039	0.66	6.3	4.4
RB4	0.063	0.99	**2.0**	**0.9**
RD4	0.067	0.71	7.7	3.2
RC5	0.040	0.97	4.1	2.8
RD5	0.104	0.99	4.7	1.2
RE5	0.025	0.47	5.4	NA
RB6	0.015	0.83	2.1	3.7
RC6	0.031	0.92	4.3	3.8
RD6	0.012	0.58	4.1	9.3
RE6	0.027	0.84	3.4	3.4
RB7	0.006	0.46	1.7	NA
RC7	0.012	0.59	2.8	6.2
RD7	0.020	0.60	4.7	6.4
LC1	0.033	0.95	**1.1**	**0.9**

Whisker	Growth rate (mm day^{-1})	r^2	Max length (cm)	Whisker lifespan (years)
LF1	0.038	0.44	10.3	NA
LA2	0.005	0.46	2.2	NA
LB2	0.006	0.24	4.3	NA
LC2	0.176	0.99	**1.4**	**0.2**
LD2	0.033	0.18	14.4	NA
LF3	0.030	0.54	6.2	5.7
LD4	0.036	0.63	6.2	4.7
LE4	0.038	0.62	6.2	4.5
LF4	0.012	0.56	2.3	5.1
LD5	0.017	0.47	4.6	NA
LE5	0.051	0.62	5.5	3.0
LB6	0.026	0.86	2.4	2.5
LC6	0.015	0.56	3.6	6.7
LD6	0.035	0.63	4.9	3.9
Nemo				
RB1	0.023	0.83	4.4	5.4
RC1	0.046	0.84	6.2	3.6
RB2	0.029	0.93	5.2	4.9
RF2	0.031	0.59	10.3	9.1
RB3	0.015	0.76	6.0	10.7
RE3	0.184	0.99	**7.0**	**1.1**
RA4	0.022	0.58	1.7	2.1
RB4	0.007	0.35	5.1	NA
RB6	0.083	0.99	**2.1**	**0.7**
RC6	0.009	0.32	4.1	NA
RE7	0.049	0.63	4.5	2.5
LC1	0.043	0.59	7.2	4.6
LE1	0.087	0.47	18.3	NA
LB2	0.022	0.72	5.9	7.5
LD2	0.140	0.79	**4.8**	**0.9**
LA3	0.013	0.52	2.2	4.7
LB4	0.014	0.59	3.7	7.5
LC5	0.020	0.68	3.9	5.3
LE5	0.020	0.57	5.5	7.6
LA6	0.008	0.73	0.7	2.5
LB7	0.004	0.27	2.2	NA
LE7	0.022	0.49	3.2	NA
LC8	0.013	0.96	1.1	2.2
LE8	0.032	0.93	1.9	1.6
Cali				
RA1	0.016	0.55	3.0	5.1
RB1	0.044	0.61	4.3	2.7
RA2	0.021	0.56	2.7	3.6
RA3	0.011	0.61	1.8	4.5
RF3	0.095	0.83	8.0	2.3
RA5	0.017	0.64	0.9	1.5
RB5	0.018	0.48	2.5	NA
RB6	0.031	0.93	2.4	2.1
LB1	0.030	0.83	4.4	4.0

Whisker	Growth rate (mm day^{-1})	r^2	Max length (cm)	Whisker lifespan (years)
LA2	0.004	0.49	1.9	NA
LB2	0.074	0.81	5.4	2.0
LC2	0.035	0.52	10.3	8.2
LA5	0.008	0.54	1.1	3.7

*Maximum length and estimated age before whisker was lost

A.2. Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) in sequential segments of whiskers collected from ten free-ranging adult female California sea lions. Values are separated by sea lion (C2 - C22), with the first column corresponding to δ^{13}C values (‰) and the second to δ^{15}N values (‰). Whisker segments are numbered from base to tip, with one corresponding to the base of the whisker and the highest number corresponding to the tip of the whisker.

	C2		C3		C5		C8		C12		C14		C16		C18		C20		C22	
1	-15.7	17.5	-15.7	17.3	-15.7	17.8	-15.3	18.4	-15.5	18.4	-16.1	18.3	-15.7	18.7	-15.6	18.8	-15.9	17.1	-15.6	17.8
2	-15.5	16.8	-15.3	17.1	-15.1	16.9	-14.9	17.8	-15.9	17.3	-16.2	17.4	-15.4	17.7	-15.8	18.1	-15.8	17.2	-15.5	16.9
3	-15.5	16.7	-15.3	17.0	-15.1	16.7	-14.8	17.6	-15.6	16.9	-16.2	17.2	-15.5	17.6	-15.3	17.5	-15.8	17.2	-15.7	17.0
4	-15.6	16.8	-15.2	17.0	-15.5	16.7	-14.8	17.7	-15.5	16.9	-16.3	17.4	-15.5	17.5	-15.3	17.5	-15.6	17.1	-15.3	16.9
5	-15.6	16.8	-15.2	17.0	-15.3	16.6	-14.7	18.0	-15.9	17.2	-16.2	17.2	-15.3	17.4	-15.4	17.4	-15.7	17.2	-15.4	16.9
6	-15.7	16.7	-15.1	17.0	-15.4	16.6	-14.8	17.6	-15.7	17.0	-16.2	17.3	-15.5	17.5	-15.5	17.4	-15.6	17.3	-15.4	17.1
7	-15.8	16.8	-15.3	17.1	-15.3	16.6	-15.1	17.6	-15.8	17.3	-16.0	17.4	-15.5	17.7	-15.5	17.6	-15.6	17.3	-15.5	17.0
8	-16.0	16.9	-15.2	17.3	-15.3	16.8	-15.2	17.6	-15.8	17.4	-15.8	17.3	-15.5	17.7	-15.5	17.8	-15.7	17.0	-15.6	17.0
9	-15.7	17.0	-14.9	17.3	-15.4	16.8	-15.2	17.2	-15.6	17.2	-15.8	16.9	-15.6	18.0	-15.5	17.7	-15.7	17.1	-15.6	17.1
10	-15.5	16.9	-14.7	17.1	-15.5	17.1	-14.9	17.5	-15.6	17.0	-15.9	17.1	-15.6	18.0	-15.6	17.9	-15.5	17.6	-15.5	17.1
11	-15.2	17.1	-14.9	17.0	-15.6	16.9	-14.4	17.7	-15.6	17.1	-16.1	17.4	-15.4	18.0	-15.3	17.8	-15.4	17.8	-15.4	17.0
12	-14.9	17.3	-14.9	17.0	-15.6	16.5	-14.4	17.5	-15.3	17.1	-16.1	17.4	-15.4	17.9	-15.1	17.9	-15.2	17.8	-15.0	16.8
13	-14.5	17.4	-15.1	16.8	-15.6	16.6	-14.5	17.1	-15.2	17.1	-15.9	17.4	-15.3	17.9	-14.8	17.9	-15.1	17.8	-14.7	16.8
14	-14.4	17.3	-14.7	16.8	-15.4	16.6	-14.7	17.0	-15.1	16.9	-15.8	17.3	-15.2	18.0	-14.9	17.7	-15.1	17.8	-14.7	16.8
15	-14.6	17.2	-14.9	16.8	-15.1	16.6	-15.0	17.0	-15.0	16.9	-16.1	17.4	-15.1	17.8	-15.0	17.9	-15.1	17.7	-14.8	16.9
16	-14.9	17.2	-14.7	16.9	-14.9	16.5	-15.3	16.9	-14.9	16.9	-16.1	17.2	-15.1	17.8	-15.0	18.0	-15.4	17.7	-15.0	17.0
17	-15.5	17.3	-14.6	17.4	-14.8	16.6	-15.7	16.9	-15.1	16.7	-15.9	17.2	-15.0	17.7	-15.2	18.0	-15.4	17.5	-15.2	16.8
18	-16.0	17.4	-14.5	17.4	-15.5	16.6	-15.7	16.7	-15.3	16.6	-15.8	17.3	-15.0	17.8	-15.3	17.8	-15.6	17.3	-15.2	16.8
19	-16.3	17.3	-14.5	17.4	-15.2	16.7	-15.7	16.7	-15.6	16.5	-16.0	16.9	-15.0	17.8	-15.3	17.7	-15.6	17.2	-15.3	16.6
20	-16.3	17.2	-14.5	17.4	-15.0	16.7	-15.8	16.5	-15.9	16.6	-15.8	16.9	-15.2	17.4	-15.3	17.7	-15.6	16.8	-15.4	16.5
21	-16.2	17.1	-14.7	17.4	-15.2	16.8	-15.9	16.6	-16.0	16.9	-15.8	17.0	-15.5	17.4	-15.4	17.7	-15.7	16.6	-15.4	16.4
22	-16.3	16.9	-14.8	17.2	-15.4	16.7	-16.2	16.6	-16.1	16.4	-16.0	16.6	-15.5	17.1	-15.4	17.9	-15.2	16.6	-15.6	16.3
23	-16.2	16.8	-15.1	16.7	-15.3	16.7	-16.3	16.3	-16.3	16.1	-16.5	16.2	-15.9	16.9	-15.4	17.6	-15.0	16.7	-15.9	16.3
24	-16.1	16.9	-15.3	16.7	-15.3	16.6	-16.7	15.9	-16.0	16.5	-16.5	16.4	-15.7	16.8	-15.2	17.4	-15.1	17.5	-16.1	16.3
25	-16.0	16.9	-15.4	17.1	-15.7	16.3	-16.7	16.2	-15.7	16.8	-16.2	16.6	-15.8	17.0	-15.0	17.7	-15.2	17.7	-15.9	16.4
26	-16.2	16.3	-15.4	17.0	-15.8	16.2	-15.6	17.2	-15.5	16.8	-15.9	17.4			-14.9	17.8	-15.3	17.6	-15.8	16.4
27	-16.0	16.3	-15.3	16.9	-16.0	16.6	-15.1	17.7	-15.7	17.3	-16.0	17.7			-15.1	17.6	-15.5	17.2	-16.1	16.0
28	-15.4	16.7	-15.3	16.6	-16.0	16.7	-15.1	17.8	-15.7	17.2	-16.2	17.9			-15.2	17.5	-15.5	17.1	-16.3	15.8
29	-15.0	17.3	-15.8	16.4	-16.2	15.9	-15.4	17.7	-15.8	17.1	-16.1	17.8			-15.4	17.1	-15.3	16.9	-16.1	16.2
30	-15.2	17.4	-15.6	16.3	-15.2	16.5	-15.6	17.4	-15.7	16.7	-16.1	17.5			-15.5	17.1	-15.3	16.9	-15.6	16.6
31	-15.8	17.2	-15.3	16.5	-15.8	16.3	-15.8	17.4	-16.0	16.6	-16.1	17.3			-15.5	16.9	-15.5	16.9	-15.6	16.7
32	-16.1	17.0	-14.7	17.2	-15.5	16.1	-16.0	17.3	-16.0	16.2	-16.0	16.9					-15.3	17.0	-15.8	16.6

	C2		C3		C5		C8		C12		C14		C16		C18		C20		C22	
33	-16.1	16.7	-14.8	17.2	-16.3	16.0			-16.4	16.3	-16.1	16.8					-15.4	16.4	-15.9	16.6
34	-16.1	16.4	-14.7	17.2	-16.4	15.8					-16.2	16.7					-15.7	16.2	-15.9	16.5
35			-14.9	17.3							-16.1	16.2					-15.4	16.8	-16.0	16.4
36			-15.2	17.3													-14.9	17.8	-16.1	16.3
37			-15.4	17.2													-14.9	17.7	-16.1	16.5
38			-15.6	16.8															-16.1	16.7
39			-15.9	16.5															-16.1	17.0
40			-16.2	16.3																

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