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SANTA CRUZ

FORAGING ECOLOGY OF MALE CALIFORNIA SEA LION (*ZALOPHUS CALIFORNIANUS*): MOVEMENT, DIVING AND FORAGING BEHAVIOR, AND DIVING CAPACITY

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Michael Joseph Weise

June 2006

The Dissertation of Michael Joseph Weise
is approved:

Professor Daniel P. Costa, Chair

Professor Terrie M. Williams

Professor James T. Harvey

Associate Professor Raphael M. Kudela

Lisa C. Sloan
Vice Provost and Dean of Graduate Studies

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Foraging Ecology of Male California Sea Lion (*Zalophus californianus*): Movement, Diving and Foraging Behavior, and Diving Capacity

Michael Joseph Weise

Abstract

I investigated diving behavior, movement, and spatially explicit foraging behavior of the sexually dimorphic male California sea lion and evaluated the extent to which blood and muscle oxygen storage capacity influenced behavioral patterns. Satellite-linked dive recorders were used to investigate the movement and diving patterns of 25 sub-adult and adult male California sea lions during 2003-04 and 2004-05. Male diving behavior was consistent with that of a typical shallow epipelagic to mesopelagic foraging strategy and a strong diurnal pattern. Variation in diving behavior was explained by the presence of three diving strategies among individuals including shallow, mixed depth, and deeper divers. Males dispersed, rather then a previously described migration, traveling north and south while foraging almost exclusively over the continental shelf during short trips in 2003-04. Ocean conditions were highly anomalous in 2004-05 and males altered their foraging effort during previously undocumented offshore excursions up to 450km offshore. Trips during 2004-05 were more than twice the distance and three times the duration of trips during 2003-04. Diving patterns also shifted with increased search time underwater with deeper and longer duration dives, and significant shifts in diet occurred that reflected changes in the diet during the 1997-98 El Niño.

I also examined the extent to which blood and muscle oxygen stores varied as a

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function of age, body size, and sex. Blood oxygen storage capacity was not fully developed by the end of the dependency period and muscle stores were not developed until animals were sub-adult size. Decreased myoglobin in adult males resulted in decreased mass-specific oxygen stores compared to females, which was unexpected given their greater body mass. Delayed development of body oxygen stores coupled with differences between the sexes resulted in different aerobic diving capacity among different size, age, and sex animals. Males dove well within their physiological diving capacity the majority of the time. This apparent excess in physiological dive capacity may provide male sea lions with the plasticity to develop alternative individual foraging strategies, and buffer them against fluctuations in prey distribution and abundance resulting from environmental perturbations such as those observed during 2005 and El Niño events.

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Enclosure and squeeze cage design was graciously provided by Robert DeLong and Pat Gearin at the National Marine Mammal Laboratory. Captures and scat collection on the Año Nuevo Island, and later, the maintenance of the floating platform in the Monterey harbor required logistical and diver support, so special thanks to Pete Dalferro for not only his assistance but his willingness to help at every turn. Also, thanks to other divers including Brett Long, Steve Clabuesch, Traci Fink, and Nate Moore. Logistics of conducting captures and regular scat collections and population counts on Año Nuevo Island required a huge amount of effort. I am grateful to Pat Morris for guidance, logistical support, and dedication to conducting counts and scat collection on the island. A component of this work was to establish baseline health parameters/indices of the free-ranging sea lion population that was done in collaboration with the Marine Mammal Center in Sausalito, California. So, I would like to thank Francis Gulland, in particular, for her advice and assistance on multiple fronts, and Denise Grieg, Christy McKnight, and Judy Lawrence who handled and analyzed blood samples. Also, thanks to Yann Tremblay for assistance with Matlab, Andreas Walli for assistance with GIS, Shawn Kramer for training me on the myoglobin assay, and Leo Ortiz for the use of his lab.

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Introduction

California sea lion is the most abundant apex predator within the California Current system with an estimated 237,000 to 244,000 sea lions in U.S. waters (Carretta et al. 2005), and an additional 44,000 to 53,000 animals in Mexico (Aurioles-Gamboa & Zavala-Gonzalez 1994). The population, occurring from offshore islands in Mexico north to Vancouver Island, Canada has the largest population of any sea lion species in the world and has increased steadily throughout the latter part of the twentieth century growing at 5% to 6.2% per annum since the passage of the Marine Mammal Protection Act in 1972 (NMFS 1997, Carretta et al. 2005). California sea lions are a sexually dimorphic otariid with adult males reaching up to four times adult female size. Sea lions give birth from late May through late June each year followed by breeding in June and July on islands off southern California and western Baja California. Following the breeding season, most sub-adult and adult males were thought to migrate northward to Oregon and Washington (Bartholomew 1967, Mate 1975). Adult female sea lions remain in the area of breeding rookeries throughout lactation until pups are weaned at six to 11 months (Melin 1995). During spring, most subadult and adult males return to breeding rookeries in southern California and western Baja California. Other than the general timing and directional movements of subadult and adult males during migration nothing was known about their at-sea distribution and diving behavior.

California sea lions compete with almost all commercial and recreational fisheries along the California coast by directly interacting with fisheries causing

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entanglement and damage to fishing gear and loss of catch (Beeson & Hanan 1996, NMFS 1997, Weise & Harvey 2005), and indirectly by competing for fisheries resources (Harvey 1987, Olesiuk 1993, Weise 2000). Recent revisions of the U.S. Magnuson Fishery Conservation and Management Act, vigorous implementation of the U.S. Endangered Species Act, and the enactment of the California Marine Life Management Act of 1998 have placed a new emphasis on restoring the health of coastal ecosystems and fisheries resources. Critical needs for attaining a healthy ecosystem are the restoration of over-harvested and/or threatened and endangered fishery populations, identification of essential fish habitats, and the evaluation of the role of predators in marine ecosystems. Although interactions occur between sea lions and commercial fisheries, dynamics of how and if these interactions regulate predator and prey populations and affect fisheries and ecosystem structure remain unknown.

In recent years, a number of federal and state natural resource agencies have begun to integrate principles of ecosystem-based management into their organizational philosophy, policy, and structure. A key component of ecosystem-based fisheries management (EBFM) is considering trophic interactions among fished and unfished species that have the potential to lead to changes in harvest or management strategies (Field et al. 2001). Further, to integrating EBFM into present management structure requires incorporating spatially dynamic information on the dynamics of predator and prey species, and understanding the influence of climate driven processes on the abundance and distribution of prey species (Field et al.

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2001). From a management perspective, the goals of this project in relation to EBFM was to evaluate and quantify the trophic interactions of the California sea lion, determine their movement and spatially explicit foraging behavior along the coast, and evaluate how these apex predators respond to climate-driven changes in the California Current System.

Our understanding of the foraging ecology of size dimorphic otariids (sea lion and fur seal) is almost exclusively derived from studies of at-sea movement and diving behavior of smaller adult females, with just seven foraging studies of adult males from four species (Green 1997, Hindell & Pemberton 1997, Boyd et al. 1998, Campagna et al. 2001, Kirkwood RJ et al. 2002, Page et al. 2005). When lactating, all otariid females are central place foragers, alternating periods at sea foraging with periods ashore on breeding rookeries provisioning pups (Bonner 1989, Costa 1991). The ease of handling and the ability to recover instrumentation has made lactating female otariids the subject of intense investigation (Shaffer & Costa 2006). Studies of adult male otariids, however, have been limited because of their large size and unpredictability of their rookery attendance. Recently, novel data compression techniques also have enabled the transmission of detailed dive behavior over extended temporal and spatial scales without the need to recover the instrument (Fedak et al. 2001, Fedak et al. 2002).

Body size is one of the most important factors shaping the ecology of animals, and is one of the more powerful tools used in predicting many life-history, morphological, and physiological traits (Peters 1983, Schmidt-Nielsen 1984).

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Among diving marine vertebrates, dive depth and duration show a strong relationship with body mass that is consistent across taxonomic groups (Schreer & Kovacs 1997, Halsey et al. 2006). It is unlikely that body mass directly increases diving ability, but that body size correlates with traits, bodily functions, or processes that likely do. For diving animals some of the more important correlates are the isometric relationship between body mass and oxygen storage capacity, and the allometric relationship between body mass and the rate at which oxygen is used (exponent 0.67-0.75; Butler and Jones 1982, Halsey et al. 2006). According to the oxygen storage/usage hypothesis (Butler & Jones 1982), therefore, larger animals should be able to dive deeper and longer than smaller animals.

Male California sea lions are a good model for testing relationships between body size and diving behavior because they are an abundant predator of strategic importance to fisheries management and we know little nothing about their behavior. This project will first define the foraging and diving behavior of California sea lions, and then relate this spatially explicit behavior to their movement on the coast and relationship with oceanographic environment. As oceanographic conditions change we would expect prey assemblages to change, so this study will concurrently investigate sea lion food habits. Lastly, in order to understand the capability of sea lion to respond to shifts in ocean productivity, this study will examine the oxygen stores and dive capacity of different age-classes and sexes of sea lion.

My specific objectives were first to describe the diving behavior and foraging strategies of male sea lions in comparison to predicted behavior based on body size.

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Second, examine movement patterns and spatially explicit foraging behavior of males following the breeding season, and evaluate changes in behavior during the 2005 warm water anomaly. The first two objectives were achieved by analyzing diving and position data collected by satellite linked depth recorders attached to the dorsal pelage of male sea lions captured in Monterey, California: the diving work is presented in chapters 1 and 2.

The third objective was to compare shifts in foraging behavior and movement patters during the anomalously warm water conditions in 2005 to spatial shifts in coastal sea surface temperature and productivity. To achieve this objective I compared monthly changes in diving patterns and effort to monthly changes in sea surface temperature in the region along the coast with the greatest concentration of diving effort during 2003-04. The fourth objective was to evaluate changes in sea lion diet relative to changes in foraging strategies in response to environmentally induced changes in prey distribution and availability. Annual variation in sea lion diet in central California was examined through the identification of prey hard parts found in fecal samples collected at Año Nuevo Island. The results of objectives 3 and 4 are presented in chapter 2. Finally, I examined the extent to which blood and muscle oxygen stores varied as a function of age, body size, and sex in California sea lions. To achieve this last objective, I measured total body oxygen stores, including hematocrit, hemoglobin, MCHC, plasma volume, blood volume, and muscle myoglobin in pups through adults of both sexes and evaluated these stores in relation to aerobic diving capacity: these results are presented in chapter 3.

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Chapter 1: Diving behavior and foraging strategies of the male California Sea Lion (*Zalophus californianus*)

Introduction

Body size is one of the most important factors shaping the ecology of animals, and is one of the more powerful tools used in predicting many life-history, morphological, and physiological traits (Peters 1983, Schmidt-Nielsen 1984). Among diving marine vertebrates dive depth and duration show a strong relationship with body mass that is consistent across taxonomic groups (Schreer & Kovacs 1997, Halsey et al. 2006). It is unlikely that body mass directly increases diving ability, but that body size correlates with traits, bodily functions, or processes that likely do. For diving animals some of the more important correlates are the isometric relationship between body mass and oxygen storage capacity, and the allometric relationship between body mass and the rate at which oxygen is used (exponent 0.67-0.75; Butler and Jones 1982, Halsey et al. 2006). According to the oxygen storage/usage hypothesis (Butler & Jones 1982), therefore, larger animals should be able to dive deeper and longer than smaller animals.

Our understanding of the foraging ecology of size dimorphic otariids (sea lion and fur seal) is almost exclusively derived from studies of at-sea movement and diving behavior of smaller adult females, with just seven foraging studies of adult males from four species (Green 1997, Hindell & Pemberton 1997, Boyd et al. 1998, Campagna et al. 2001, Kirkwood et al. 2002, Page et al. 2005b). When lactating, all

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otariid females are central place foragers, alternating periods at sea foraging with periods ashore on breeding rookeries provisioning pups (Bonner 1989, Costa 1991). Fitness in lactating otariids will not always be optimized by feeding in the most productive regions, but by milk delivery rates to their dependent pups (Bryant & Turner 1982). The ease of handling and the ability to recover instrumentation has made lactating female otariids the subject of intense investigation (Shaffer & Costa 2006). Male otariids are not involved in parental care and can maximize their fitness by searching further afield for the most productive regions. Studies of adult male otariids, however, have been limited because of their large size and unpredictability of their rookery attendance. Recently, novel data compression techniques also have enabled the transmission of detailed dive behavior over extended temporal and spatial scales without the need to recover the instrument (Fedak et al. 2001, Fedak et al. 2002).

Sexual dimorphism is evident among marine mammals and may lead to differences in foraging strategies and ecology of the larger sex. Based on the (Kleiber 1961) relationship between body mass and metabolic rate the absolute metabolic requirements increased with body mass, therefore, larger individuals required more energy per unit time than smaller individuals. Increased energetic intake may require different foraging strategies for individuals of the larger sex (Clutton-Brock et al. 1982, Ginnett and Demment 1997). In sexually dimorphic species, the greater energetic requirement of the larger sex could lead to the smaller sex being out-competed if both sexes use similar foraging strategies in the same area

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consuming the same food types. As niche-divergence hypothesis predicts, in areas where male and female foraging locations overlap the sexes may reduce competition by consuming different prey (Schoener 1969, Hughes 1980, Williams 1980, Clarke et al. 1998). Alternatively, niche divergence may result in animals foraging on similar diets but in different places. Males and females also may forage differently because of differences in the sex-specific energetic costs of reproduction. In mammals, the energetic expenditure of females during gestation and lactation often outweigh the expenditure of males in acquiring mates and defending resources during the same period (Gittleman & Thompson 1988, Perrigo 1990, Wilkinson & Barclay 1997). These hypotheses are not mutually exclusive when examining the foraging strategies and diving behavior of marine birds and mammals.

In sexually dimorphic pinniped species differences between male and female foraging distribution and diving behavior have been identified and related differences in body size, niche separation, and costs of reproduction. Male elephant seals (*Mirounga* sp.), which are up to ten times greater in mass than females, forage in different areas and depths than females (Le Boeuf et al. 2000). In grey seals (*Halichoerus grypus*), seasonal differences in dive behavior between the sexes were attributed to sexual dimorphism, but more importantly, differences in the costs and benefits of stored energy for reproduction (Beck et al. 2003). In Antarctic fur seals (*Arctocephalus gazella*), males dived deeper and in different areas than females because of sub optimal or local depletion of resources by females (Boyd et al. 1998). Male and female New Zealand fur seals (*A. forsteri*) used different prey species and

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dramatically different foraging strategies to maximize their survival and reproductive success (Page et al. 2005a). Male otariids typically foraged further afield, spent longer times at sea, and dove deeper than females (Page et al. 2005a).

California sea lions are a sexually dimorphic otariid distributed along the West Coast of North America with adult males reaching up to four times adult female size. Breeding occurs in June and July on islands off southern California and Mexico. Following the breeding season, most sub-adult and adult males disperse northward to central and northern California (Weise 2006, Chapter 2), and possibly as far as Oregon and Washington (Bartholomew 1967, Mate 1975). Adult female sea lions remain in the area of breeding rookeries throughout lactation until pups are weaned at six to 11 months (Melin 1995). Sea lions are the most abundant apex predator in the California Current System (Carretta et al. 2002), consume predominantly commercially important fish species (Lowry et al. 1990, Lowry et al. 1991, Lowry & Carretta 1999, Weise 2000, Weise & Harvey In Review), and interact and potentially compete with most fisheries along the California coast (Weise & Harvey 2005). Key to understanding trophic interactions within coastal ecosystems along the west coast of North America is insight into the foraging ecology of this large and abundant apex predator. Despite a long history of research on this species, investigations of diving behavior have been limited to a few studies on adult females at rookeries in southern California (Feldkamp et al. 1989, Kuhn 2006).

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In this study we examined the diving and foraging strategies of male California sea lions following the breeding season along the West Coast of North America. Because of the considerably greater size of males in this species and resultant increase in energetic demands we expected male sea lions to spend longer at sea, and dive deeper for greater durations than previously studied females. Lastly, we investigated whether the lack of parental care by males allowed for niche divergence between the sexes leading to males to foraging differently than females further from rookeries. To examine these hypotheses we recorded male sea lion diving behavior using satellite-linked time-depth recorders.

Methods

Animal Handling

Eighteen adult and seven sub-adult male California sea lions were captured and instrumented in the municipal harbor of Monterey, California (36°36.5' N, 121°53.4'W) during September through December 2003 and November and December 2004 using an aluminum enclosure (3m x 4m x 2m) and squeeze cage (2.5m x 1m x 1.5m; R. DeLong, National Marine Mammal Lab, pers. comm.). The enclosure was situated on a floating platform (4m x 8m) and secured to the United States Coast Guard wharf at the base of the rock jetty where animals normally come ashore (haul-out) to rest. Captures involved the voluntary entry of sea lions into the enclosure, ensuring a random sample of the population, followed by the triggering of a sliding door to enclose the animals. Animals were transferred to a squeeze cage,

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physically restrained, sedated with Midazolam intramuscularly at 0.20mg kg^{-1} (mixed with atropine at 0.02 mg/kg) and then anesthetized with isoflurane gas (0.5 to 5% w/O_2). Isoflurane was delivered at 5 to 15L min^{-1} oxygen flow using a circle rebreathing circuit (Heath et al. 1997) via gas mask or intubation. Once quiescent, lengths and girths (±0.5cm) were measured and mass was determined with a digital hanging scale (±0.5 kg; Dyna-Link MSI–7200). During 2003, 22 satellite-relay data loggers (SRDL 7000, 11cm x 7cm x 6cm, Sea Mammal Research Unit (SMRU), University of St. Andrews, Scotland) were attached to the pelage dorsally between the shoulder blades at the point of maximum girth using Devcon™ 5-minute epoxy. In 2004, three conductivity-temperature-depth tags (CTD, SMRU, 11cm x 7cm x 7cm) were attached on the back of the head using Loctite™ 5-mintue epoxy. Once recovered from anesthesia the animals were released from the capture platform. Tags had a frontal area of 32.0cm, which based on the mean frontal area of tagged sea lions, mean swim speed, and drag coefficient for California sea lions (Feldkamp 1987) increased the drag and power required for swimming sea lions by 1.9%; therefore, size of tags had a negligible impact on animal.

Satellite relay data logger programming

Data on sea lion behavior and environment were collected by the SRDL, summarized, and transmitted via the ARGOS satellite system when the animal was at the surface. Data from the first three SRDLs deployments were used to optimize the subsequent data acquisition algorithm, thereafter the minimum depth for a dive was set at 5.5m for a duration of 10s. For every dive, start and end time were

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recorded and tags recorded dive depth (±0.5m) and duration (±1s), and surface interval sampled every 4s. Additionally, summaries of percentage time spent in different behavioral states for every four-hour period were transmitted to build a comprehensive picture of dive behavior. Summary data included behavioral states: diving (>5.5m and 10s), swimming at the surface (<5.5m and 10s), and hauled out, number of dives, mean, SD, and maximum diving depth and duration. Start and end time of all haul-out periods also was recorded. Speed across the surface (horizontal) was calculated between each satellite position based on the great-circle distance between locations and the time elapsed (McConnell et al. 1992). All data were stored in a transmission buffer for four days, before being deleted from tag memory. Data were transmitted every 45 seconds when the tag broke the surface of the water and at intervals of 80 pulses per second during the first five hours of each haul-out period. While the animal was in the water, surface swimming was recorded if no dives were recorded for six minutes. A haul out period began after the tag was dry for six minutes and ended after the tag was wet for 40 seconds. During haul-out periods the tags cycled 'on' for three hours, and 'off' for two hours with a maximum of 500 transmissions per day. Because this was the first time SRDLs were deployed on male sea lions we set the tags to collect more data early in the deployment with the tag set to transmit 60,000 times the first 100 days, and 80,000 times by 300 days. All time variables were collected in Greenwich Mean Time (GMT) and corrected for local time based on the geographic position of the sea lion at that time.

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The SRDLs provided a combination of randomly sampled 'profile dives', which in addition to depth and location, recorded water temperature (±0.1°C) every four seconds during one of the two deepest dives every two hours during each 24-hour period. CTD tags deployed in 2004 were programmed to almost exclusively collect 'profile dives' including temperature, conductivity, and depth. Detailed profiles were collected during the deepest dive every hour, with a minimum depth of 200m resulting in limited overall dive information. Filtering and compression was performed by the conventional broken-stick method used for standard oceanographic XBTs cast and produced 12 temperature-depth pairs. The ability to interpret how sea lions used their environment depended on having concomitant oceanographic data of sufficient quality and resolution. Animal-derived oceanographic data were collected at a spatial and temporal scale, relevant to the animal's foraging behavior, and allowed comparison of diving and foraging behavior in relation to features such as the thermocline.

Diving Patterns and Effort

Diurnal patterns in diving behavior were examined by transforming data to local time, pooling dive data from all animals, and calculating the mean of dive parameters for each hour of the day. Activity patterns and diving frequencies were determined only from those days in which data were received for all 4 hour summary periods. Activity pattern (percentage time hauled out, swimming or diving) were arcsin transformed before analysis. Start and end times for each haul

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out period were transformed to local time, and trip duration was calculated by subtracting end time of haul out period from start time of the next haul out period.

Habitat Usage

Habitat was defined as the region of diving activity within the water column relative to the depth of the thermocline and distance from the seafloor. Thermocline was estimated using the IKNOS toolbox (Y. Tremblay, unpublished) by interpolating between the 12 temperature-depth pairs at 1m intervals, and identifying a change in temperature gradient of 0.05° C/m over a minimum of three consecutive temperature points in either direction. Least-squares regression was fitted to thermocline depth versus diving depth for all dives with temperature profiles, and residuals (difference between dive depth and regression line) from this relationship were used to compare individual animals' diving behavior relative to the thermocline. To examine diving in relation to the seafloor, we compared dive depth and seafloor depth as determined using the ETOPO2 Global 2' elevations (Smith & Sandwell 1994).

Individual Foraging Strategies

Principal component analysis (PCA) was used to reduce the number of behavioral variables used to characterize and compare foraging strategies among individuals. This analysis reduced the number of behavioral variables from 22 to 12 variables and collapsed these into a few dominant, orthogonal axes. The appropriate number of components to extract was selected using the *i*) latent root criterion, which states that only factors with eigenvalues of 1 or above would be included and

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ii) the criterion that more than 5% of the variance be explained (Hair et al. 1995, McGarigal et al. 2000). Collinearity among variables was eliminated by collapsing variables into uncorrelated orthogonals. Hierarchical cluster analysis of the factor scores from the PCA was used to detect discontinuous groupings or "clumps" of data points in multidimensional space (McGarigal et al. 2000), which were interpreted to represent distinct foraging strategies. Distance measure used was the square of the Pearson product-moment correlation (r^2), as this measure maximized the cophenetic correlation coefficient and thus best represented the raw data structure (Gauch 1982, McGarigal et al. 2000). Ward's minimum variance method was used to link similar points, and the number of significant clusters was determined by graphical examination of the resulting dendrogram and scree plot of inter-cluster distance versus the number of clusters (McGarigal et al. 2000). A discriminat analysis was then used to evaluate the effectiveness of classifying each individual into a cluster or foraging strategy, and identify the key variables that contributed most to the classification. Insufficient dive data were collected for animals in 2004-05 so they were not included in this analysis.

Summary data are reported as mean ± SD, unless otherwise noted. Differences between means were tested using a two-sample *t*-test, and relationships were tested using least-squares linear regression analysis. Comparisons of the distribution of individual diving patterns in northern and southern California were tested using a two-sample Kolmogorov-Smirnov test, and differences between mean dive parameters were

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compared using a paired *t*-test. Multivariate analysis was done with Matlab 7.0, and all other statistical analysis was conducted using SYSTAT 10 (SPSS Inc. 2000).

Results

Animal handling and tag performance

Twenty-five male California sea lions were captured and instrumented in the Monterey harbor during 2003 (n=22) and 2004 (n=3), seven were sub-adults (110.9 kg, n=7) and eighteen were adult males (183.7 kg; Table 1). From May 2003 to February 2004, temperature-only SRDL tags remained attached for 23 to 127 days logging 51,920 dives and 1,781 temperature profiles. From late November 2004 through March 2005, CTD tags remained attached for 98 to 118 days and logged 2,447 dives and 68 temperature profiles. The use of different epoxy and/or mounting site (head vs. back) may have increased the duration of tag deployments in 2004-05 (106±14 days) compared with 2003-04 (44±24 days; Table 1).

Dive performance and patterns

Mean dive depth for all male sea lions was 32 m (± 44) and mean dive duration was 1.9 min (± 1.6). Mean dive depths of individuals ranged from 19 m to 96 m, with 86% of all dives less than 50m (Table 2, Fig. 1a). Only 2.5% of dives were greater than 150 m, with two individuals exceeded 450 m. Mean dive durations of individuals was 0.8 to 3.4 minutes (Table 2), the maximum dive duration exceeded 10.0 minutes for three individuals. Frequency distribution of dive depth indicated a leptokurtic distribution with a peak at 10 to 20m decreasing steadily with greater

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depths (Fig. 1a). Frequency distribution of duration also was leptokurtic with peaks at 30 to 60s dive durations decreasing slightly to two minutes and then dropping sharply thereafter (Fig 1b). The deepest single dive recorded was 475m, which was from a different individual than the greatest dive duration of 12.1 minutes. Dive duration increased with diving depth on an individual basis (r^2=0.43, P=0.001; Fig. 2a), and for all individuals and all dives combined (r^2=0.52, P<0.001). Among individuals, surface interval was positively related with diving depth (r^2=0.63, P<0.001; Fig. 2b), and diving duration (r^2=0.29, P=0.012; Fig. 2c).

In general, males spent an approximately equal time hauled out (49.7%) and at sea (51.3%). While at sea animals spent 62.0% of their time swimming at the surface, and the remainder diving (36.1%; Table 2). There was no relationship, however, between deeper dives and the percentage time spent diving while at sea (r^2=0.00, P=0.975; Fig. 3a) or at the surface swimming (r^2=0.09, P=0.176; Fig. 3b). Because males dove to relatively shallow depths (32 m) it was not surprising that the mean dive rate did not decrease significantly with increasing dive depth (r^2=0.16, P=0.075).

Increasing body mass of males was positively related to dive duration (r^2=0.31, P=0.009; Fig. 4a) negatively related to time at sea (r^2=0.22, P=0.034; Fig. 4b) and positively related to time hauled out (r^2=0.22, P=0.034; Fig. 4c). Body mass had no affect on diving depth among individuals (r^2=0.01, P=0.696). There also was no relationship between body size and either trip duration (r^2=0.14, P=0.097),

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percentage of time at sea spent diving (r^2=0.05, P=0.313), or percentage of time spent surface swimming (r^2=0.17, P=0.067).

In general, diving occurred at all times of day although strong diurnal patterns were apparent. Whereas variability was high when dive behavior was pooled for all individuals, there was decreased mean frequency of dives, shallower dives, decreased duration of dives, with increased surface intervals during nighttime hours approximately between the hours of 1800 and 0600 local time (Fig. 5a, b, c, d).

Habitat use

In-situ temperature profiles were recorded by the SRDL along the track of each animal. Within and among individuals there was a significant relationship between diving behavior and thermal structure of the water column. Males dove deepest where thermocline depth was greatest (r^2=0.10, P<0.001), and mean dive depth of individuals increased as thermocline depth increased (r^2=0.80, P<0.001; Fig. 6). Interestingly male diving behavior was more strongly associated with near-surface oceanographic features than bathymetry (Fig.7). Such a diving pattern is consistent with an epipelagic foraging strategy as described for adult female sea lions (Feldkamp et al. 1989, Costa et al. 2001, Costa et al. 2004).

Nine males returned to southern California during the non-breeding season and I compared their diving behavior when they were north (northern California) and south (southern California) of Pt. Conception (34.45° N, 120.47° W). While in southern California the distribution of animal diving depth, duration, and surface interval was significantly greater for 7 out of 9 individuals for depth and duration,

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and 6 out of 9 for surface interval (K-S; $P<0.001$). Mean dive duration of individuals while in southern California was significantly greater (3.3±2.3 min; Paired t-test, $t=5.754, P=0.001$), although dive depth (64±94 m; Paired t-test, $t=1.385$, $P=0.215$) was greater the difference was not significant. Distribution of percentage time diving was significantly different in 6 of 9 males (K-S; $P<0.001$). Mean percentage time diving (24.8±28.7 %) was greater while males were in southern California compared with their behavior while in northern California (18.5±23.9%; Paired t-test, $t=-0.762$, $P=0.475$), although the difference was not significant.

Comparisons of males while in southern California versus northern California were confounded by the fact that animals were in different locations during different time periods. Comparisons of males that did not return to southern California, however, for the same time periods when males were in southern California (time period 1) versus northern California (time period 2) showed no changes in the distribution or mean dive depths, durations, or the percentage time spent diving.

Individual foraging strategies

Principal components analysis indicated that 81.1% of the variation among individuals in diving behavior could be explained by three factors (Table 3); diving patterns (PC1), foraging effort (PC2), and surface behavior (PC3). PC1 explained 41.6 % of the variance, and was composed of mean and SD of dive depth, duration, and habitat use defined by mean and SD of ratio of dive depth to thermocline depth. PC2 explained 22.6% of the total variance and was composed of dive frequency, trip

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duration, and percentage of time spent at sea, and PC3 was composed of surface interval and horizontal swim speed and explained 17.0% of the total variance.

Hierarchical cluster analysis of the three principal components indicated that individuals could be classified into three distinct groups based on their diving behavior (Fig. 8). Individual sea lions also were easily partitioned into the three distinct behavioral grouping by discriminant analysis (Fig. 9), and jack-knife re-sampling of the data resulted in correct group assignment 86% of the time. Individuals in group 1 had the smallest body mass and were characterized by the greatest frequency of dives, dives that were the shallowest, shortest duration, closest to the thermocline, and with the shortest surface interval among the groups (Table 2). This group also spent the greatest percentage of their time at sea during the longest trips of the three groups and swam the fastest at the surface. Individuals in group 2 had less frequent, deeper dives, but the greatest duration dives farthest from the thermocline, therefore, a greater surface interval than group 1 (Table 2). This group spent less of their time at sea than group 1, and had the longest trips among all the groups. Group 3 was distinguished as the least frequent but deepest divers, far from the thermocline, and the greatest surface interval, although not the longest duration dives (Table 2). Group 3 spent the least percentage of time at sea diving and had the shortest trips.

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Discussion

Greater body size clearly influenced the diving behavior and foraging strategies of male sea lions in some of the predicted ways but not in others. Despite the greater body size in males mean diving behavior was largely consistent with a shallow epipelagic foraging strategy with a strong diurnal pattern as previously described for adult females of this species (Feldkamp et al. 1989). However, variability within and among individuals was extensive resulting in distinct individual-based foraging strategies. In fact, individuals in this study had some of the deepest (475m) and greatest duration (12.1min) dives for California sea lions, or for any otariid species. Because of the different individual strategies identified in this study the range of diving strategies for male sea lions extended from the epipelagic to mesopelagic (>200m) environment. Diurnal patterns were evident with males conducting relatively shallow dives of short duration to variable depths in relation to thermocline depth and far from the bottom during daytime hours and more frequent, deeper, and greater duration dives during nighttime hours.

Diving patterns

Mean male sea lion diving depth (32m) and duration (1.9 min) were similar to predicted values (depth, 28m; duration, 2.4 min; Halsey et al. 2006) based on mean body mass alone, although mean maximum values were much greater than predicted. Mean maximum, the mean of maximum values per individual, dive depth was 297m compared to a predicted value of 51 m, and mean maximum duration was 9.1 min compared to a predicted 3.1 min. There are a number of factors in addition

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to body size that can influence diving behavior including predator characteristics (behavior, ecological niche, reproductive status), and prey parameters (horizontal and vertical distribution, quantity, density; Butler 2004).

Occurrence of epi-mesopelagic diving strategy in males was supported by the fact that there was no increase in time spent diving or surface swimming in relation to increased dive depths. Benthic feeding otariids spend increased time diving and have increased surface intervals with increased mean dive depths that likely relate to transit time to and from foraging depths and/or pushing their physiological dive capacity (Costa et al. 2001, Costa et al. 2004). Whereas, shallow diving species have little transit time to reach foraging depths resulting in less time at sea, and these species often operate well within their capacity. Adult female Antarctic fur seals have a similar diving pattern to male California sea lions, in that they routinely make shallow dives (19m) for short durations (1.3min), and spend a similar amount of time at sea diving (20.4%; Costa et al. 2000). An additional benefit to spending a decreasing amount of time at sea diving for fur seals was a concurrent decrease in field metabolic rate (FMR). Conversely, New Zealand sea lions (*Phocarctos hookeri*) use a benthic diving strategy and demonstrate a strong relationship between increased percentage time at sea diving and increasing dive depth, spending 44 % of their time at sea diving during trips that last 4.4 days (Costa & Gales 2000). Further, at-sea FMR of New Zealand sea lions increases as the proportion of time spent diving increases. The energetic consequence of different foraging strategies is that New Zealand sea lions spend 2 to 4 time more time at sea diving with diving effort

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that is 4 to 7 times greater than Antarctic fur seals (Costa & Gales 2000). The FMR, percentage time spent diving (32.7%–41.5%), and trip duration of female California sea lions (2.5 days; Feldkamp et al. 1989, Kuhn 2006) indicate that they have a similar energetic benefit as fur seals. In males, this energetic benefit was likely greater because they spend almost half the amount of time at sea diving (18.5%), during shorter trips (0.5 days), and have a lesser mass-specific metabolic rate as a result of greater size.

Males often moved into mesopelagic waters (>200m) where they spent increased time underwater followed by increased surface intervals between dives. This pattern could be explained by pushing or exceeding aerobic diving capacity, or the need to return to the surface to handle and consume prey. Deeper longer dives may push the physiological dive capacity of animals and they may be incorporating anaerobic metabolism during the dive, which would require an increased surface interval to recover (Kooyman et al. 1980). Although this may have been possible on individual dives, few male sea lions approached their calculated aerobic dive limit even when using conservative estimates of oxygen consumption during diving (Fig. 10a). Further, there was no relationship between mean dive depth or duration as a function of mass-specific oxygen storage capacity (blood, muscle, and lungs; Fig. 10b).

Large prey species were identified in the sea lions diet (salmonids, rockfishes, and hake; Weise 2006, Chapter 2) indicating that increased surface intervals may be explained by the need to return to the surface to handle and consume larger individual prey items. During observations of sea lion interactions with commercial

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and recreational salmon fisheries in Monterey Bay, California it was common to observe adult male sea lions bring large salmon to the surface to be consumed (Weise and Harvey 2005). Further, of the larger prey species consumed by sea lions, rockfishes and hake are more typically distributed at deeper depths well below the thermocline and closer to the bottom (Chess et al. 1988, Reynolds 2003, Helser et al. 2006). Therefore, the explanation for longer, deeper dives, and increased surface intervals may be the need to bring large prey to the surface for consumption.

Sex differences and male diving patterns

It was surprising that male California sea lions made such shallow dives (32±44m) for such short intervals (1.9±1.6min) and with so little effort (36.8 % time at sea diving), especially when compared to smaller female California sea lions (studied over a similar time period) in southern California that on average dove deeper (58.2 m) for longer intervals (2.1 min), and with greater effort (41.5 % of their time diving; Kuhn 2006). Based on size alone males should be able to dive to greater depths and longer durations than observed in this study (Schreer and Kovacs 1997; Halsey et al. 2006). Two possible explanations for the inconsistency in diving pattern and effort were that males were more efficient predators than females or that males were less selective of prey than females. Mass-specific energetic requirements decrease with larger body size while gut capacity scales isometrically (Peters 1983) resulting in a ratio of gut capacity to metabolic requirements that is greater in larger animals. As suggested by Beck et al. (2003), therefore, larger male sea lions could meet their energetic requirements by digesting larger quantities of lower-quality

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prey more easily than females leading to less selective foraging behavior and presumably less diving effort. Females may be selective about prey quality to maintain lactation, thus expending greater effort to pursue more profitable prey types. Males also may have an advantage in their ability to capture and handle larger prey items

The theory of niche divergence indicates that adult male sea lions would consume different prey species than females when in the same area or that males would consume a similar diet but in a different place. Our data indicated that for most of the year males foraged in different geographic regions than females on rookeries in southern California. As all of our males were tagged in Monterey Bay they were obviously feeding in a different location than females initially. Dispersal of males was possible because they were not constrained by the need to return to the rookery to suckle the pup, whereas females foraged in close proximity to the rookery (Costa 1993). Dispersal of males northward of rookeries also may be explained by an animals ability to meet their energetic needs more efficiently (shallow dives of less duration with less overall foraging effort) in central and northern California than southern California.

Thirty-seven percent of our tagged animals returned to rookeries in southern California outside the breeding season. We could therefore compare sex specific differences diving behavior and effort of the males in southern California to females tagged on San Nicolas Island during the same season and years (Kuhn 2006). Further, we could examine whether there was a shift in the foraging behavior of

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males while they were foraging in the same area as females (southern California), as compared with areas where females were absent (northern California). While in southern California male diving behavior shifted towards the female diving pattern. In southern California males dove deeper (64 m±94.; $P<0.215$), for longer durations (3.3min ± 2.3min; $P=0.001$), and spent more of their time diving (24.8%±28.7; $P=0.769$) compared to when they were in northern California (depth, 29m±34m ; duration, 1.7min ± 1.4min; % time diving, 18.5%±23.9). Because male dive depth was similar to females in southern California, they were likely feeding on similar prey species, therefore, not exhibiting niche divergence. Although our data indicates that male and female sea lions exhibit similar diving patterns while both were present in the same region they may have foraged in different locations within the same area (Schoener 1969, Clarke et al 1998) or during different times of day (Beck et al. 2003).

Access of male otariids to females during the breeding season is dependent upon their ability to secure and defend territories, and may explain why tagged animals returned to breeding rookeries in southern California outside of the breeding season. Little data is available on male otariid movements, but Troy et al. (1997) speculated that male New Zealand fur seals occupied their territories outside the breeding season and displayed to females in an effort to influence female choice upon the arrival of the breeding season, or to display to rival males to reduce the need for physical fights during the breeding season. The majority of males in this study that returned to rookeries were adults, likely conferring upon them the selective benefits

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as suggested by Troy et al. (1997), although the breeding status of adult males captured in this study was unknown. These selective benefits conferred upon males returning to rookery sites outside the breeding season may be offset by increased diving effort and deeper dives of greater duration required to sustain them in southern California.

Individual foraging strategies

Other researchers (Feldkamp et al. 1989, Costa et al. 2004) have described California sea lions as diving epipelagically (and in some cases mesopelagically), however, this was the first study to identify alternative foraging strategies among individuals within this general pattern. The epipelagic to mesopelagic diving strategies indicated by our tagging data was consistent with the diet of California sea lions in central California during this time period (2003-04), which was dominated in mass consumed by northern anchovy (*Engraulis mordax;* 44.5%), Pacific sardine (*Sardinops sagax*; 25.6%), Pacific hake (*Merluccious productus;* 14.1%), rockfishes (*Sebastes spp.;* 11.2%), and market squid (*Loligo opalescens*; 4.6%; Weise, Chapter 2). Fisheries dependent data, while biased in some respects, can be a proxy for the abundance and distribution of prey species. Anchovy (40%) and sardine (13%) increased in relative importance in the sea lion diet during 2004 compared to 2003, which reflected increasing commercial fisheries landings in central California (anchovy 77%, sardine 22.6% increases; (Sweetnam et al. 2005). Whereas, hake (4%) and rockfish (33%) decreased in the sea lion diet, in contrast to a 172% increase in landings for hake and 19% increase for certain rockfish species

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(Sweetnam et al. 2005). Declines in market squid in the sea lion diet (10%) reflected declines (10 to 32%) in commercial fisheries landings during the same period (Sweetnam et al. 2005).

These prey species are almost all schooling, vertically migrating species, that occur over the continental shelf and shelf break in association with the thermal stratification of the water column (Morejohn et al. 1978, Vaughan & Recksiek 1978, Chess et al. 1988, Reynolds 2003, Helser et al. 2006, Hill K.T. et al. 2006). Variation in vertical distribution of these species with respect to thermal structure is related to stage of development (hake and rockfishes), physical transport mechanisms within the California Current System (CCS), and water column stratification (Ahlstrom 1959, Moser & Boehlert 1991, Dalebout et al. 2003). For example, larger adult size hake occur in 200 to 500m water during spawning, and their horizontal distribution along the coast is age-dependent. Rockfishes (*Sebastes sp.*) in the sea lion diet were not identified to species but likely consisted of pelagically schooling rockfish that are distributed in relation to water-column stratification (Dalebout et al. 2003), and demersally distributed larger rockfish species found on the shelf break. The CCS was in a 'normal' climatological state during 2003-04, remaining in a cold phase since the 1999 La Niña (Goericke et al. 2004). Prey schools are generally compact and patchily distributed, and likely account for variability in behavior among and within individual sea lions. Prey behavior also is consistent with the strong diurnal pattern in dive frequency, depth, and duration.

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Water temperatures recorded by SRDLs indicated that males dived to depths that were related to the thermal stratification of the water column, a proxy for which used in this study was thermocline depth. This behavior was not only consistent with the epipelagic foraging strategies of female sea lions (Feldkamp et al. 1989, Costa et al. 2004), but more importantly, was consistent with the known distribution of sea lion prey species relative to thermal structure of the water column (Morejohn et al. 1978, Vaughan & Recksiek 1978, Chess et al. 1988, Reynolds 2003, Helser et al. 2006, Hill K.T. et al. 2006).

The considerable inter-individual variation in diving behavior was best explained by three orthogonal axes: dive patterns, diving effort, and surface behavior. These same variables also characterized individual diving strategies using cluster analysis. Consistent with differences in body size among individual strategies, there were strong relationships between body mass and increased dive duration, decreased percentage time at sea diving, and increased percentage time hauled out.

Because males diving patterns are relatively shallow with distinct periods of diving they likely visually search for prey from the surface while swimming between patches to minimize the greater transport costs associated with diving, similar to what has been described for fur seals (Boyd 1996). Individual diving strategies, therefore, were likely reflective of foraging behavior and associated with the targeting of different types of prey distributed within specific depths of the water-column. Marine predators are likely to make decisions at the level of

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individual dives (how long to remain submerged) and at the level of patch residence (how long to remain within a patch before leaving to find another; Thompson et al. 1993, Thompson & Fedak 2001). It has been suggested that reduced diving effort (shallow and decreased duration dives) and lower relative time spent diving indicated that the individuals that spend more time swimming at the surface between patches, and thus spend less time per patch, caught more prey for their effort (Boyd et al. 1995, Arnould et al. 1996, Boyd 1996).

A common pattern among air breathing marine predators is that when many small prey must be captured during a single dive predators are restricted to diving shallow minimizing transit time. Whereas when prey are deep and a large proportion of the time is spent in transit, predators are limited to feeding on a few large prey (Costa 1991). In this study, group 1 animals exhibited shallow, short dives, followed by short surface intervals, and the most effort (frequency of dives, time at sea, trip duration) among the three groups. These animals had the smallest average body size among the groups, the majority of which were sub-adult animals. These shallow diving animals dove in close relationship to thermocline depths and likely focused their efforts on prey species such as squid, sardines, and anchovies that are distributed relatively shallow relative to the thermocline. Group 2 and 3, were large animals that were primarily adult males. The most pronounced difference between these groups was in diving effort. The reduced overall foraging effort of group 3 animals indicated a foraging strategy that was more efficient, that may be attained only in larger and possibly older and/or more experienced animals. Animals in

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group 3 had deeper dives well below the thermocline that were either mesopelagic or closer to the bottom or shelf break. It was likely that this group targeted larger individual prey items including larger rockfish species, adult size hake, and adult sardines. Behavior of group 2 may be explained by a mixed foraging strategy that was less effort (less frequent dives, less time diving, although longer trips) than group 1 but required more effort (more frequent dives, more time diving, longer trips) than group 3. It is likely that this group fed primarily on shallow, abundant, schooling prey such as squid, sardines, and anchovies, supplementing their diet with larger prey items.

In summary, body size was a good predictor of average diving patterns in male California sea lions, although maximum values for dive parameters were significantly greater than predicted. Pinniped diving behavior can be constrained by physiological oxygen stores, and maximum behavior in male sea lions may have pushed physiological limits; however, the majority of the time males dove well within their physiological diving capacity. This apparent excess in physiological dive capacity may provide male sea lions with considerable reserve capacity to alter their diving behavior and effort in relation increasing energetic demands of an upcoming breeding season, and buffer them against seasonal or annual fluctuations in prey distributions and abundance that result from environmental perturbations such as those observed during ENSO events (Trillmich et al. 1991). Different foraging strategies among individuals likely accounted for much of the variation in diving behavior among males, and likely

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reflect differences in the distribution of targeted prey. This indicates that individuals may consume prey in unequal proportions and perhaps even totally different prey. Significant differences in male diving pattern and effort in southern versus northern California indicates that targeted prey niche may vary geographically. Therefore, geographic, seasonal, annual, and individual variation in forging strategies must be considered in the context of ecosystem-based management when evaluating the impacts of a growing predator population on prey species.

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Table 1. Summary information on California sea lions outfitted with Sea Mammal Research Unit SRDL tags.

Animal ID	Age / Sex	Date of first transmission	Date of last transmission	Deployment days	Number of Dives Recorded
28587	Adult Male	6/3/2003	7/20/2003	47	1849
28588	Subadult Male	7/28/2003	9/15/2003	49	3678
28589	Subadult Male	7/28/2003	9/29/2003	63	2922
28590	Adult Male	9/23/2003	10/17/2003	24	812
37587	Adult Male	9/30/2003	10/26/2003	26	0
37588	Subadult Male	9/30/2003	10/29/2003	29	1098
37589	Subadult Male	10/6/2003	10/29/2003	23	1711
37590	Subadult Male	10/9/2003	11/17/2003	39	2051
37591	Adult Male	10/15/2003	2/19/2004	127	5459
37592	Adult Male	10/23/2003	1/8/2004	77	3470
37593	Adult Male	10/23/2003	11/23/2003	31	1332
37597	Subadult Male	11/6/2003	12/9/2003	33	1801
37598	Adult Male	11/10/2003	11/29/2003	19	1309
44632	Adult Male	11/5/2003	12/19/2003	44	2510
44633	Adult Male	10/28/2003	11/28/2003	31	1671
44634	Adult Male	11/5/2003	12/18/2003	43	2715
44635	Adult Male	11/10/2003	12/12/2003	32	1621
44636	Adult Male	11/6/2003	12/13/2003	37	1397
44637	Adult Male	11/6/2003	12/14/2003	38	2822
44638	Adult Male	11/11/2003	12/18/2003	37	1551
44639	Adult Male	11/11/2003	12/18/2003	37	1216
44640	Subadult Male	11/5/2003	1/23/2004	79	6143
26343	Adult Male	11/30/2004	3/1/2005	91	658
28588	Adult Male	11/26/2004	3/24/2005	118	774
28599	Adult Male	12/4/2004	3/22/2005	108	1015

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Table 2. Summary of mean diving patterns and effort for 25 tagged male California sea lions. Foraging strategies were determined using hierarchical cluster analysis and grouped by number (1-3). Data collected from males tagged in 2004 were insufficient to include in analysis of individual foraging strategies.

Year	Foraging Strategy	Animal ID	Body mass	Dive depth ± SD (m)	Dive duration ± SD (min)	Surface duration (min)	Dive frequency (# dives / 4 hrs)	Trip duration (hrs)	Residual dive depth to thermocline depth ± SD	Time surface (%)	Time diving (%)	Time haulout (%)
2003-04	Group 1	28588	79	24.1 ± 33.9	1.1 ± 1.0	1.1	47.5	11.3	54.3 ± 56.2	37.4	20.0	42.7
		28589	70	27.3 ± 9.3	2 ± 0.9	1.0	41.2	23.2	25 ± 30.7	31.6	34.7	33.8
		37588	119	24.3 ± 28.9	1.6 ± 1.1	1.4	32.7	13.4	49.5 ± 71.4	36.2	21.3	42.4
		37589	117	23.1 ± 15.3	1.5 ± 0.8	1.1	34.5	5.4	22.5 ± 10.8	25.5	20.6	53.9
		37590	122	31.2 ± 28.7	1.4 ± 1.0	1.6	31.5	14.7	45.8 ± 38.9	43.4	17.7	39
		37591	168	19.1 ± 21.0	1.3 ± 1.0	1.5	28.3	10.2	38.1 ± 41.7	40.2	13.6	46.3
		37592	145	30.3 ± 25.0	1.5 ± 1.0	1.4	29.4	10	30 ± 20.6	34.9	17.4	47.7
		44634	129	32.3 ± 31.5	1.8 ± 1.2	1.6	27.2	10.5	58.9 ± 58.8	37	20	43.1
		44635	156	37.3 ± 40.1	2 ± 1.4	1.8	34.3	12.3	67.8 ± 63.4	45.3	25.8	29
		Mean	**122.8**	**27.7 ± 26.6**	**1.6 ± 1.1**	**1.4**	**34.1**	**12.3**	**43.5 ± 43.6**	**36.8**	**21.2**	**42.0**
	Group 2	28587	311	37.4 ± 52.7	3.8 ± 2.6	1.5	26.9	8.8	64.1 ± 85.8	23.6	25.1	51.3
		28590	183	47.4 ± 87.2	1.7 ± 1.7	1.3	36.2	11.8	116.4 ± 117.1	37.2	18.4	44.3
		44637	200	21.7 ± 16.3	2.1 ± 1.7	1.4	27.1	10.2	37 ± 75.4	24.5	21.8	53.8
		44639	192	25.3 ± 40.2	1.5 ± 1.2	1.5	24.2	18.3	53.1 ± 90.9	29.2	15.1	55.7
		44640	124	46.6 ± 71.1	2.1 ± 1.8	1.6	26.1	15.2	108.6 ± 122.8	38.4	21.7	39.9
		Mean	**202.0**	**35.8 ± 53.6**	**2.2 ± 1.9**	**1.5**	**28.1**	**12.9**	**75.8 ± 98.4**	**30.6**	**20.4**	**49.0**
	Group 3	37593	191	22 ± 20.4	1.6 ± 1.2	1.7	18.2	9.1	60.5 ± 72.3	29.9	12.7	57.4
		37597	145	24.4 ± 21.8	1.6 ± 1.2	1.6	23.1	8	30.1 ± 19.7	26.4	15.4	58.2
		37598	202	24.3 ± 12.7	1.9 ± 1.1	1.3	22.8	4.6	22.3 ± 15.0	22.5	17.9	59.6
		44632	153	34.4 ± 29.5	2.1 ± 1.3	1.7	22.4	9.2	37.3 ± 22.3	28.7	17.7	53.6
		44633	156	28.3 ± 25.3	2 ± 1.4	1.5	23.5	8.2	45.9 ± 34.3	27.4	19.3	53.3
		44636	155	96.3 ± 103.2	3.4 ± 2.7	2.8	12.2	12.8	171.4 ± 110.9	37.9	16.8	45.3
		44638	274	39.9 ± 47.9	2.4 ± 2.0	2	17.7	10.1	65.8 ± 78.9	32.2	17.3	50.5
		Mean	**182.3**	**38.6 ± 37.7**	**2.1 ± 1.6**	**1.8**	**20.0**	**8.9**	**61.9 ± 50.5**	**29.3**	**16.7**	**54.0**
2004/05		26343	163	33.7 ± 44.2	1.6 ± 1.7	1.8	35.4	44.4	na	51.4	20.5	28.0
		28588	178	52.1 ± 64.4	2.5 ± 2.2	2.6	22.4	50.2	na	33.7	15.5	50.8
		28599	191	50.7 ± 62.8	2.7 ± 2.7	2.5	24.1	45.8	na	48.9	17.3	33.8
	Overall Mean			**45.5 ± 57.8**	**2.1 ± 1.8**	**2.3**	**27.3**	**46.8**		**44.7**	**17.8**	**37.5**

Table 3. Component loadings of 12 variables of diving behavior on the first three components, which collectively explained 81.1 % of the total variance in the data. Parameters accounting for most of the variability in each principal component are shown in bold. PC1 related to dive patterns, PC2 to diving effort, and PC3 to surface behaviors.

	Variables	PC1 41.6%	PC2 22.6%	PC3 17.0%
1	Mean dive depth	**0.778**	0.054	0.515
2	SD of dive depth	**0.905**	0.118	0.232
3	Mean dive duration	**0.705**	-0.347	0.198
4	SD of dive duration	**0.914**	-0.308	0.129
5	Mean surface interval	0.543	-0.252	**0.723**
6	Mean horizontal swim speed	0.138	0.09	**0.849**
7	Mean of diving depth to thermocline depth	**0.870**	0.142	0.359
8	SD of diving depth to thermocline depth	**0.876**	0.154	-0.003
9	Mean trip duration	0.294	**0.730**	-0.176
10	Frequency of dives	-0.299	**0.725**	-0.414
11	Mean time spent at sea (%)	0.167	**0.861**	0.226
12	Body mass	0.431	**-0.748**	-0.197

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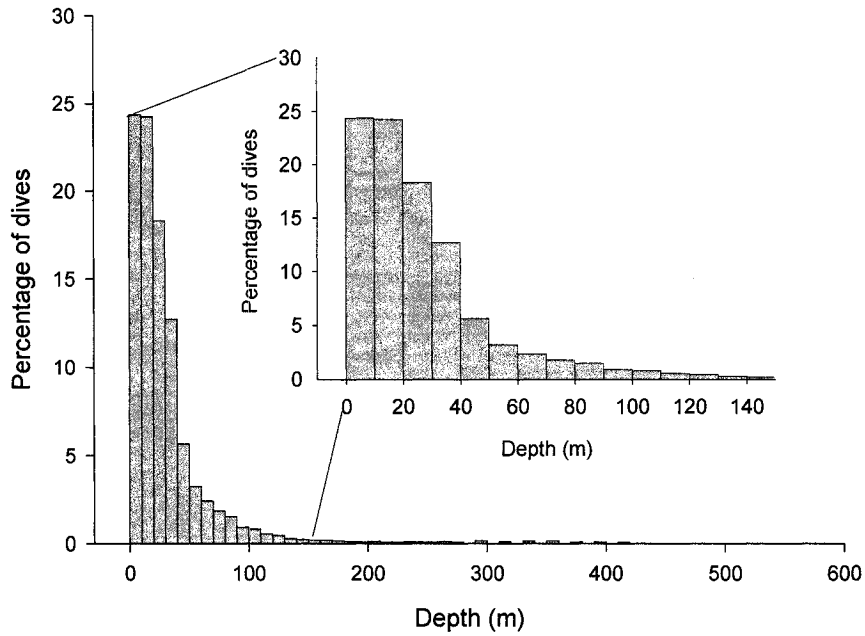

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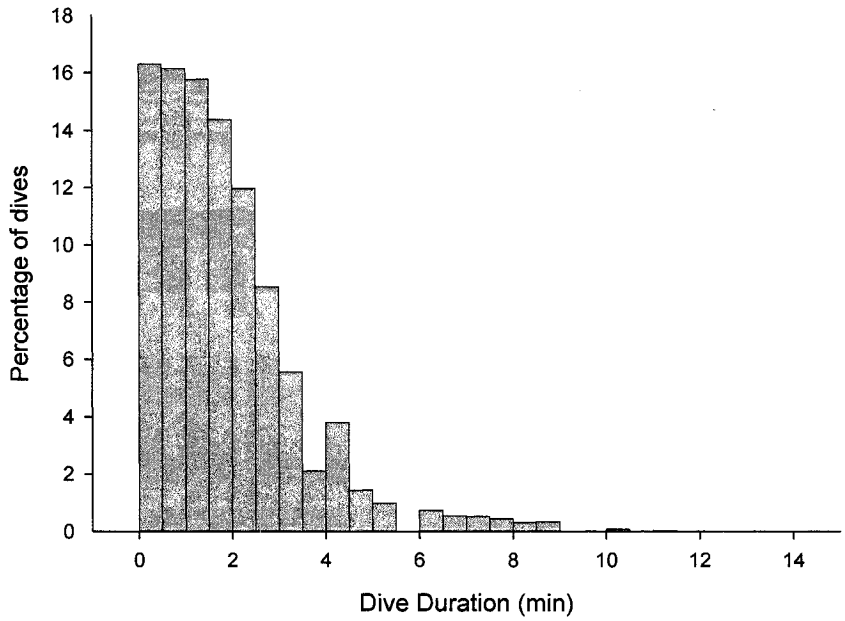

Figure 1. Frequency distribution of the percentage of dives by a) full range of depth, and depth less than 150m (insert) and b) duration for twenty-one male sea lions tagged in Monterey, California in 2003 and 2004.

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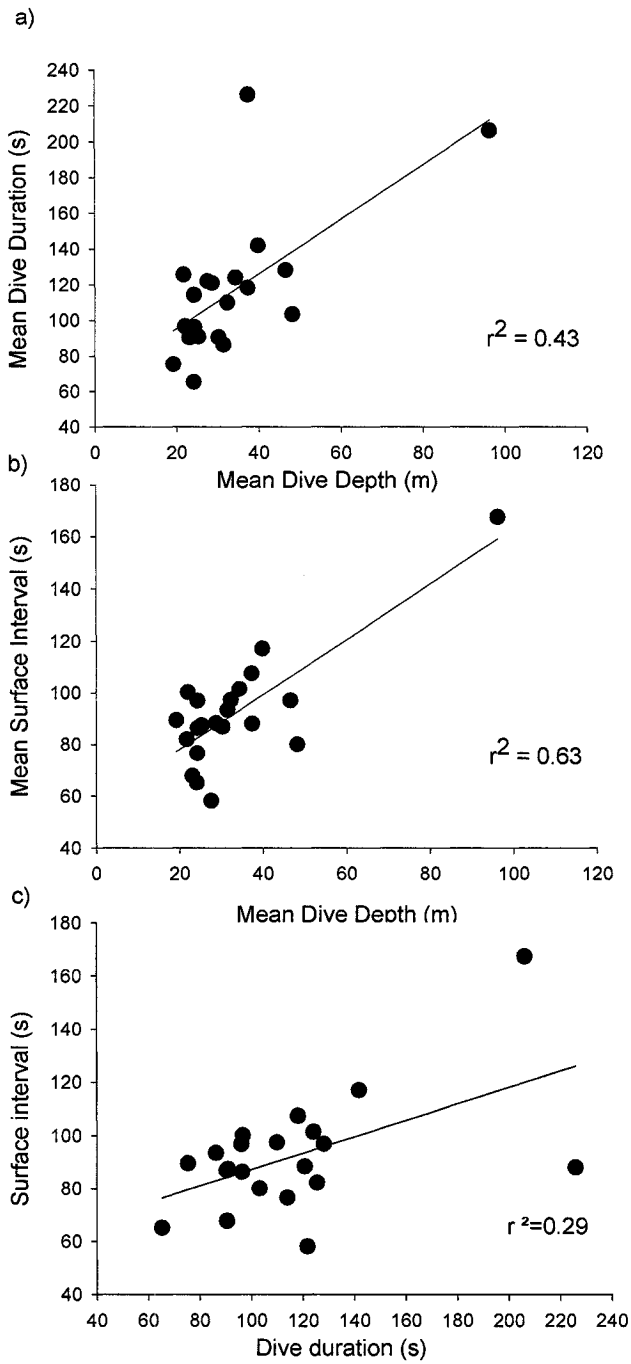

Figure 2. a) Mean dive duration and b) surface interval as a function of mean dive depth for each animal. Fig. 2c) surface interval as a function of dive duration for each individual. Lines indicate a significant relationship between mean dive depth and mean dive duration (r^2=0.43, P=0. 001), and mean surface interval (r^2=0.63, P<0. 001), and between dive duration and surface interval (r^2=0.29, P<0. 012).

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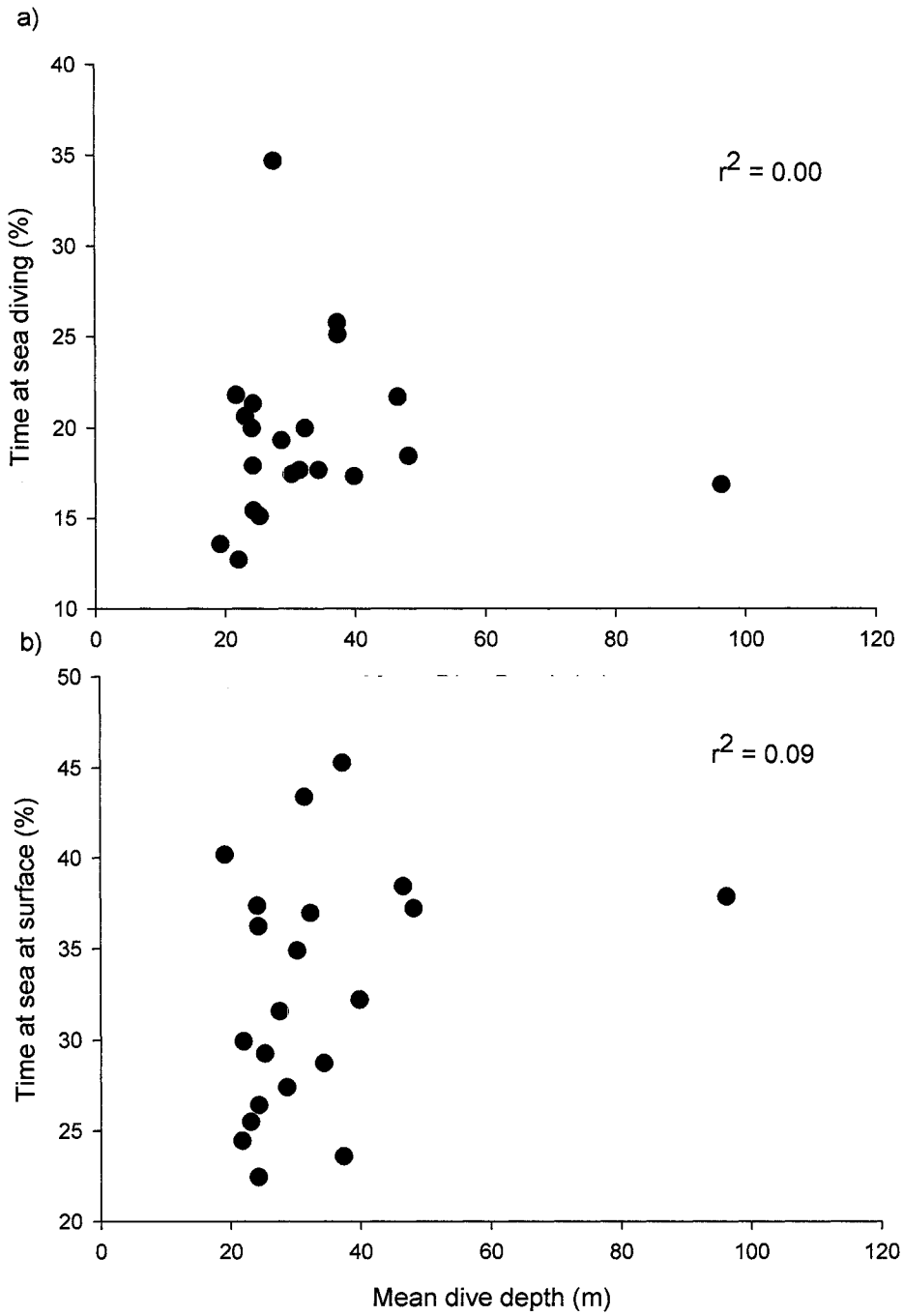

Figure 3. Mean proportion of a) time at sea spent diving (>5.5m for 10s), and b) time at sea swimming at the surface (<5.5m and 10s) as a function of dive depth for each individual sea lion. There was no relationship between mean dive depth and the percentage time spent diving (r^2=0.00, P=0. 975) or time swimming at the surface (r^2=0.09, P=0. 176).

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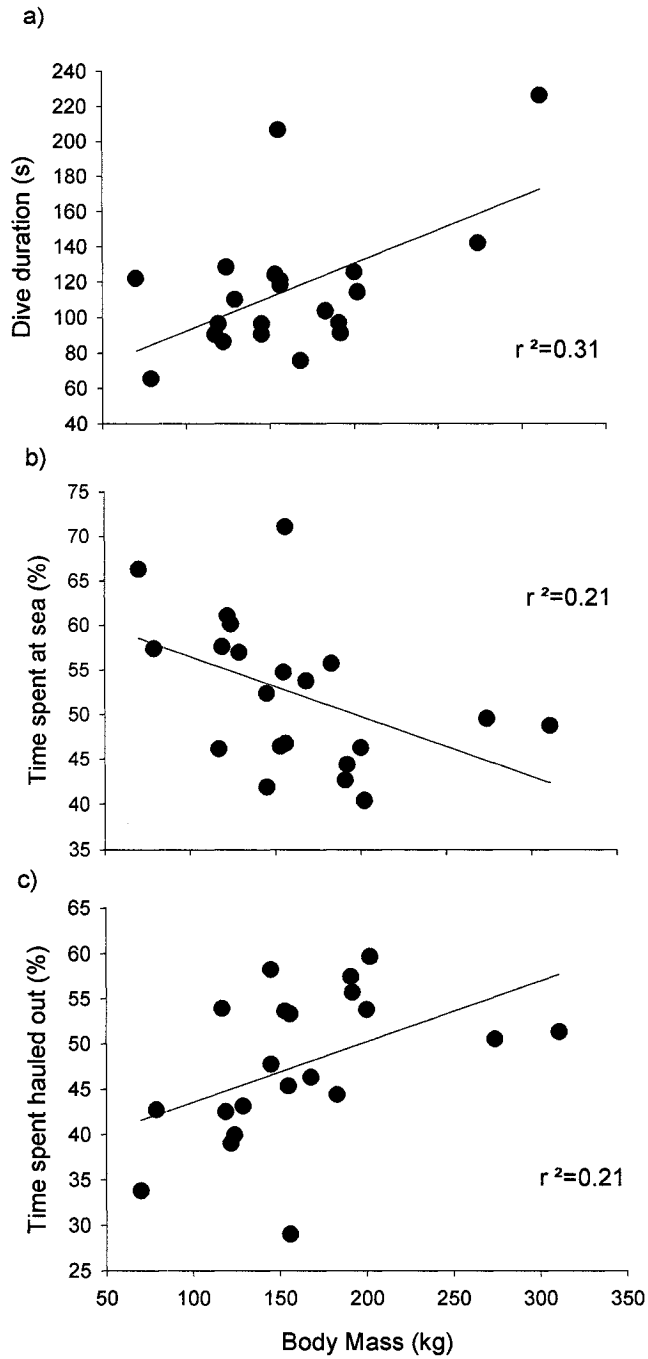

Figure 4. Relationship of mean a) dive duration, b) time spent at sea (diving and surface swimming combined), and c) time on land hauled out; as a function of body mass for each individual sea lion. Lines indicate a significant linear relationship between body mass and dive duration (r^2=0.31, P=0. 009), time spent at sea (r^2=0.21, P=0. 034), and time haul-out on land (r^2=0.21, P=0. 034).

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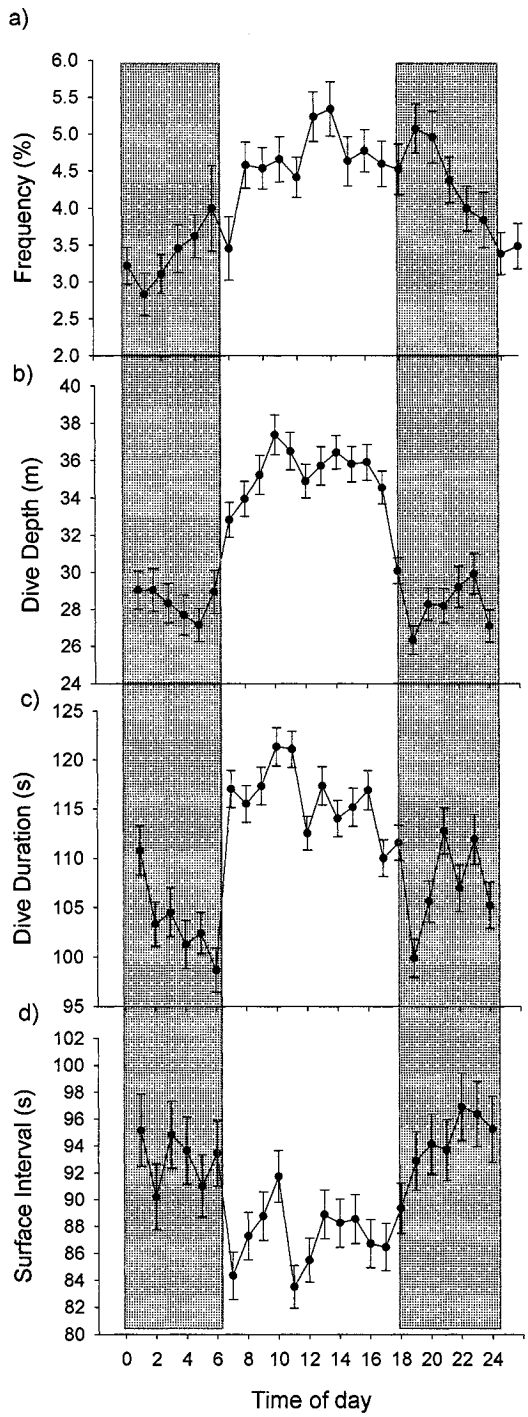

Figure 5. Diurnal patterns in diving behavior based on hourly means (±SD) during daytime (no shading) and nighttime hours (shaded) for a) frequency of dives per four-hour summary period, b) diving depth, c) diving duration, and d) surface interval.

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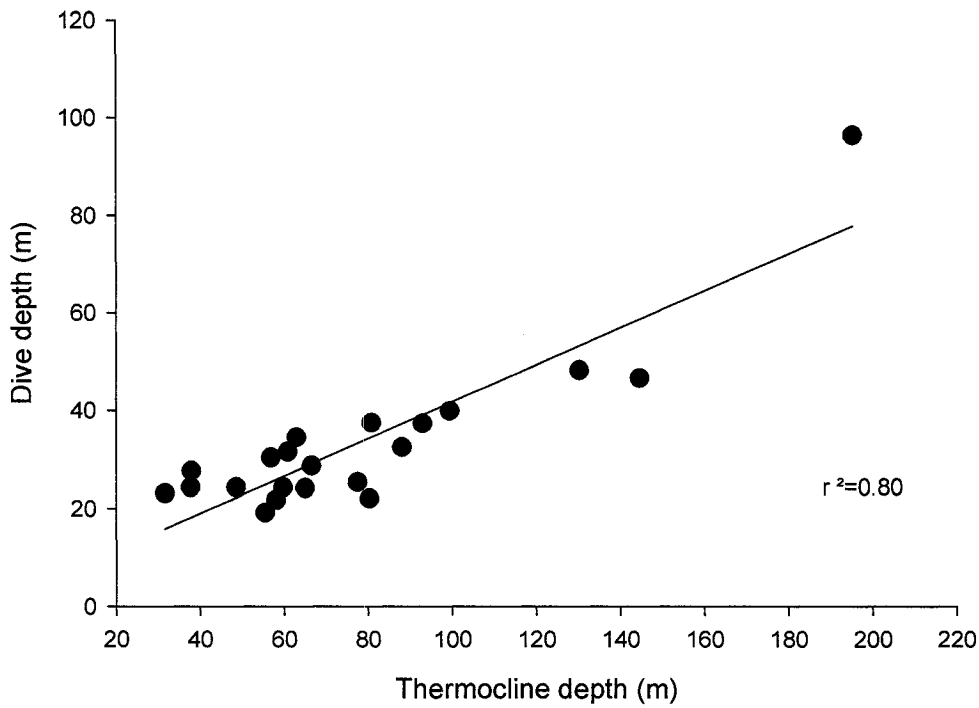

Figure 6. Relationship between mean diving depth and thermocline depth for each individual. Thermocline was calculated using *in-situ* temperature data collected by the SMRU tag.

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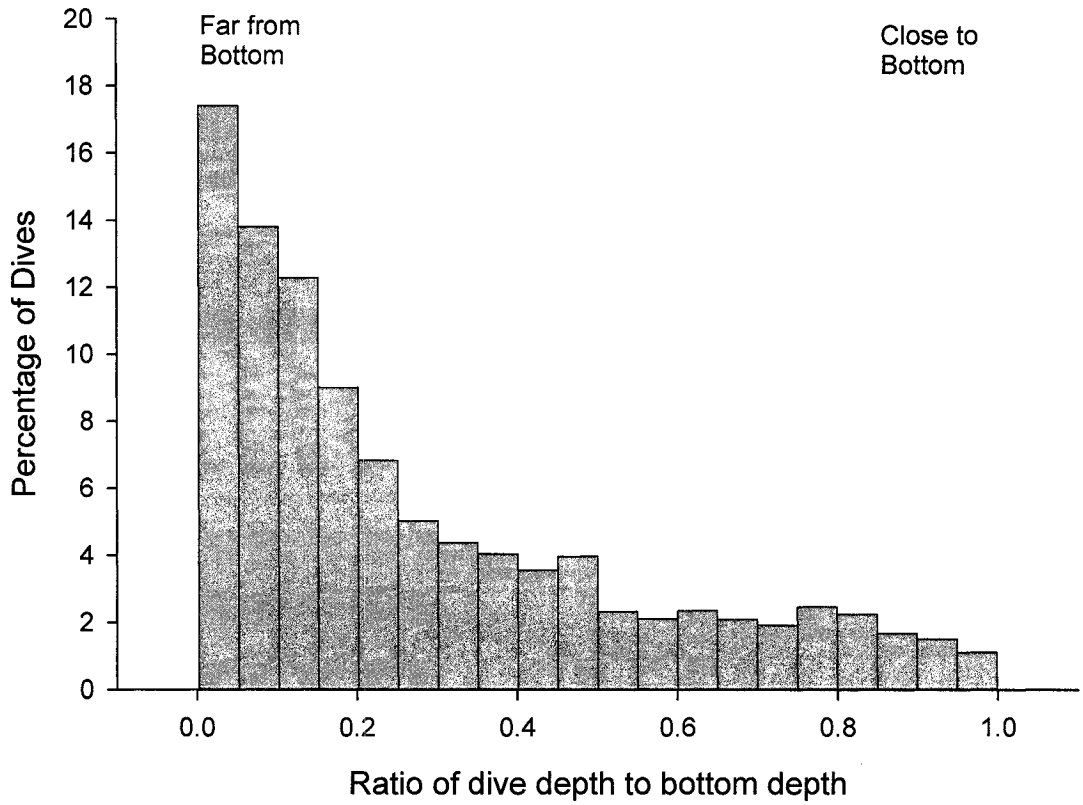

Figure 7. Frequency histogram of the percentage of dives based on the ratio of diving depth to bottom depth for all dives and all animals. A ratio closer to 0.0 is far from the bottom indicating dives in surface waters, and a ratio closer to 1.0 was closer to the bottom indicating dives toward the benthos.

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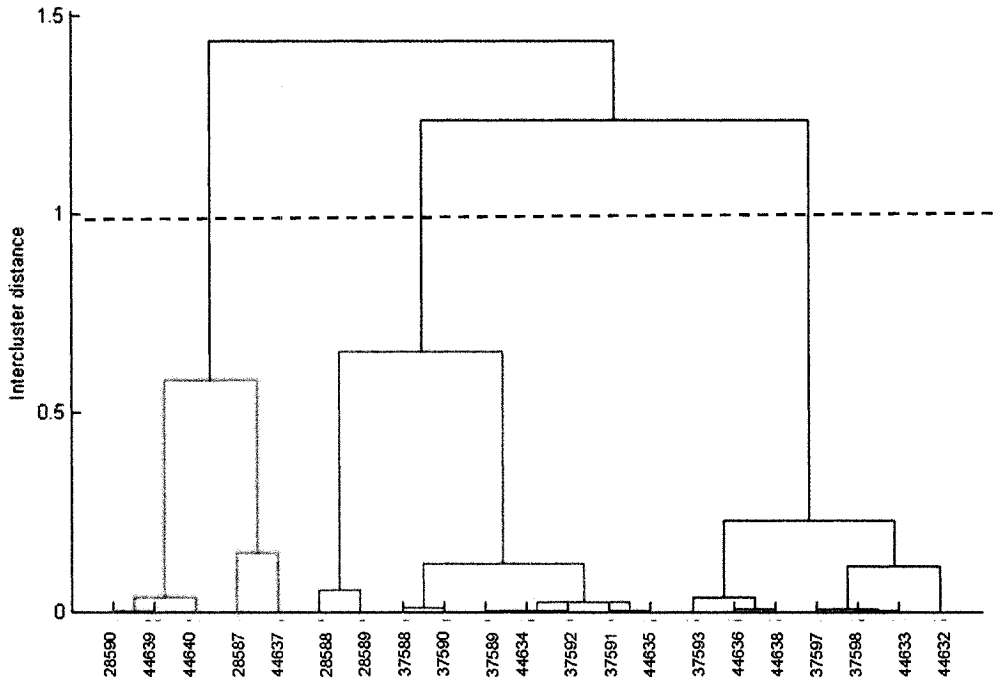

Figure 8. Result of the cluster analysis used to detect natural grouping in diving patterns, diving effort, and surface behaviors among individual male sea lions based on 12 variables. Dendogram shows hierarchical relationships between individual animals with branch length indicating the relative distance between adjacent nodes. The dashed horizontal line shows the cut-off point selected resulting in 3 different clusters representing different foraging strategies (green, red, blue).

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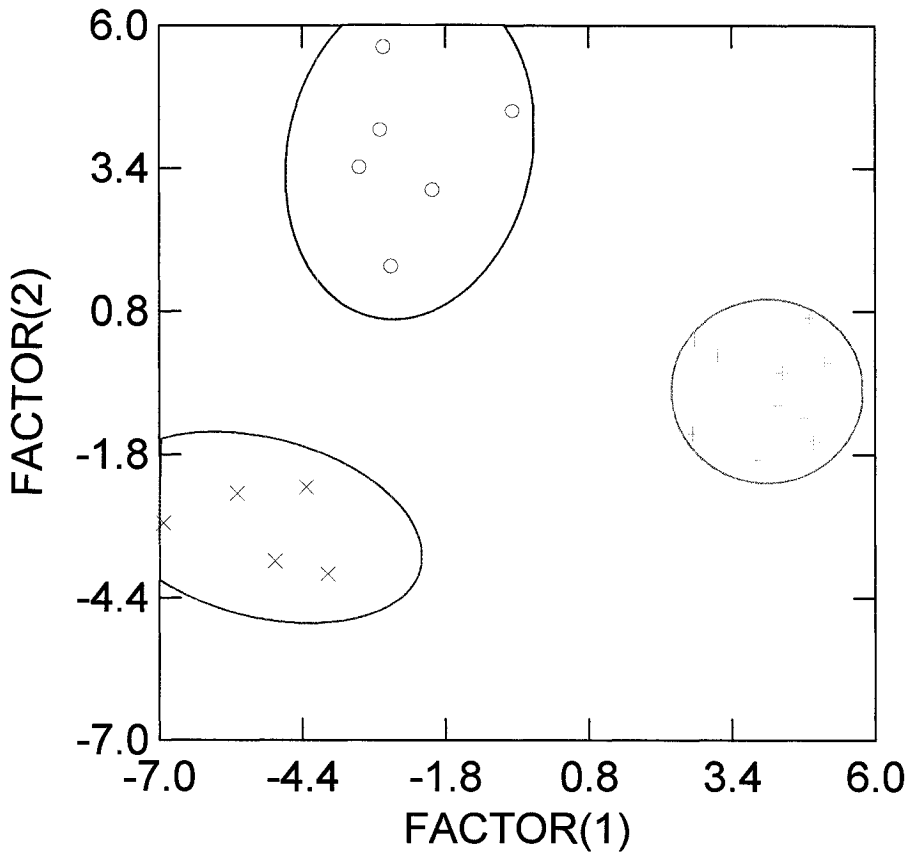

Figure 9. Plot of discriminant function analysis scores of two canonical variables showing the overall clumping of individuals into different groups distinguishing foraging strategies. Jack-knife re-sampling of the data resulted in correct group assignment 86% of the time.

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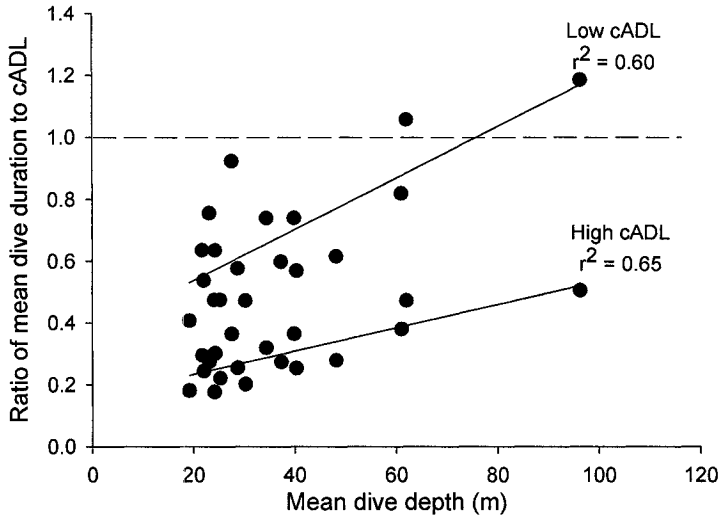

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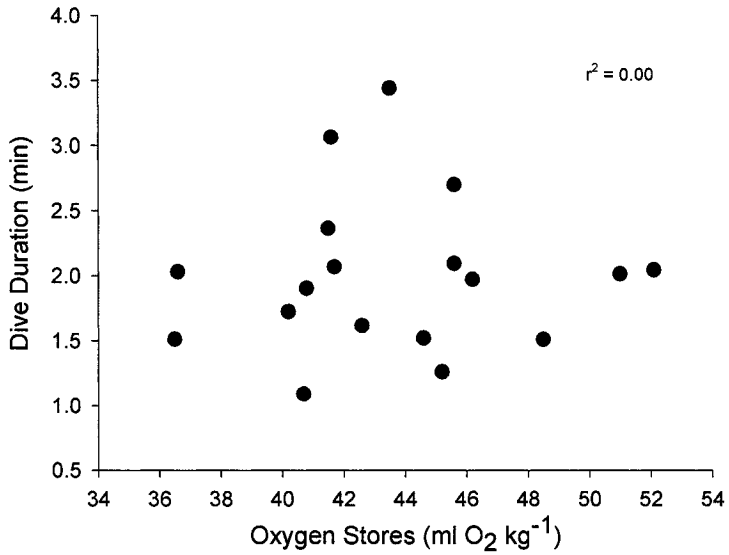

Figure 10. Diving performance of male California sea lions relative to their oxygen storage capacity and aerobic diving limit (ADL). a) Dive performance defined as the ratio between mean dive duration and the calculated aerobic dive limit (cADL, Weise 2006, Chapter 3) as a function of diving depth for all individuals. b) Relationship between diving duration as a function of the mass-specific oxygen storage capacity in the blood, muscle, and lungs combined for all individuals. ADL was calculated using two estimates of metabolic rate, high metabolic rate resulting in low cADL and low metabolic rate resulting in high estimate of cADL. Dashed line represents the ADL.

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Chapter 2. At-sea movement and diving behavior of male California sea lion (*Zalophus californianus*) during 2004 and 2005

Introduction

Distribution, abundance, and behaviors of top marine predators are related to oceanographic features, primary productivity, and distribution and abundance of prey (Guinet et al. 2001, Croll et al. 2005, Crocker et al. 2006). Marine resources are distributed heterogeneously in space in time and are often associated with oceanographic features such as frontal systems, thermal layers, seamounts, and continental shelf breaks (Schneider 1982, Haney 1986, Costa 1993, Decker & Hunt 1996). Apex predators forage in areas where these oceanographic features increase the availability of prey (Hui 1979, Schneider 1982, Springer & Roseneau 1985, Haney 1986, 1991, Elphick & Hunt 1993, Decker & Hunt 1996, Hunt 1997). All of these oceanographic features and processes are thought to drive bottom-up forcing that impacts marine predator distributions by physically forcing prey aggregations and, thus, creating areas where foraging efficiency can be increased (Ainley & Jacobs 1981, Croxall et al. 1985, Boyd & Arnbom 1991, Veit et al. 1993, Wilson et al. 1993).

Marine mammals have evolved diverse life history patterns to accommodate fluctuations in the physical and biological environment (Costa et al. 1989, Trillmich et al. 1991, Costa 1993, Costa et al. 1996, Crocker et al. 2006). As they are long-lived animals they must be able to withstand variations in food resources over large spatial and temporal scales. A basic understanding of the foraging behavior and

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habitat utilization of predators requires knowledge of this spatial and temporal variation, coupled with information on how organisms respond to these changes.

Our understanding of predator associations with marine habitat is primarily limited to population level studies where animal abundance has been correlated with oceanography. While these studies are informative they cannot provide insights into the strategies employed by individual animals nor can they provide insights into the spatial or temporal course of these interactions (Gilbert & Erickson 1977, Joiris 1991, Ribic et al. 1991, Veit et al. 1993, Bester et al. 1995, Boyd 1996, Trathan et al. 1998). Recent advances in technologies such as satellite telemetry, satellite-linked depth recorders, and remote sensing methods are providing new insights into the links between predators, prey, and the oceanic environment (Costa 1993, Boehlert et al. 2001, Fedak et al. 2001, Block et al. 2002, Fedak et al. 2002).

The coastal marine ecosystem along the West Coast of North America is characterized by the large scale California Current System (CCS), a major eastern boundary current, and considered one of the major upwelling regions in the world (Husby & Nelson 1982, Brink 1983, Schwing et al. 1991), which varies seasonally both spatially and temporally (Schwing et al. 1991). Additionally, CCS waters are subject to large-scale, long-term processes associated with E Niño Southern Oscillation (Hayward 1993, Lenarz et al. 1995, Chavez 1996, Ramp et al. 1997, Schwing et al. 1997, Lynn et al. 1998). Frequency, duration, and seasonal cycle of short-term changes (upwelling) and long-term changes in oceanographic conditions (El Niño) has important effects on productivity and community structure of lower

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and middle trophic levels, and hence top-trophic level distribution and abundance (Horne & Smith 1997, Saunders & McFarlane 1997, Lynn et al. 1998, Hayward et al. 1999).

In this study we examine male California sea lions (*Zalophus californianus*) foraging behavior and how individuals alter this behavior in response to annual changes in oceanographic features and distribution of prey within the CCS. Population level changes in California sea lion abundance, foraging energetics, and food habits have been documented during periods of fluctuations in prey distributions and abundance resulting from environmental perturbations such as those observed during ENSO events (Trillmich et al. 1991, Sydeman & Allen 1999). However, outside of females on breeding rookeries in southern California little to nothing is known about movement and diving behavior of males nor their response to environmental perturbations.

Following the breeding season (May through late June), male sea lion movement northward to central and northern California, Oregon, and Washington has been described as a migration (Bartholomew 1967, Mate 1975). During spring, most sub-adult and adult males return to breeding rookeries in southern California and western Baja California. Spring and summer of 2005 normal upwelling favorable winds were suppressed due to the blockage of the jet stream resulting in the latest onset of upwelling on record (Schwing et al. In Review). Consequently, anomalously elevated surface water temperatures and changes in the distribution and abundance of prey species were greater than during El Niño conditions (Brodeur et al. In

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Review). Here we investigated changes in the movement patterns, diving behavior, and diet of male sea lions during the 2005 warm water anomaly.

Methods

Animal Handling

Eighteen adult and seven sub-adult male California sea lions were captured and instrumented in the municipal harbor of Monterey, California (36°36.5' N, 121°53.4'W) during September through December 2003 and November and December 2004 using a modified aluminum enclosure (3m x 4m x 2m) and squeeze cage (2.5m x 1m x 1.5m). The enclosure was situated on a floating platform (4m x 8m) and secured to the United States Coast Guard wharf at the base of the rock jetty where animals normally haul out on land to rest. Captures involved the voluntary entry of sea lions into the enclosure followed by the manual triggering of a sliding type door to enclose the animals. Animals were transferred to the squeeze cage where they were physically restrained and if necessary sedated with Midazolam intramuscularly at 0.20mg/kg (mixed with atropine at 0.02 mg/kg) in conjunction with isoflurane gas (0.5 to 5% w/O_2) or with isoflurane alone.

Data Collection

During 2003, 22 satellite-relay data loggers (SRDL, Sea Mammal Research Unit (SMRU), University of St. Andrews, Scotland) were attached dorsally to the pelage between the shoulder blades using Devcon^{TM} 5-minute epoxy. In 2004, three conductivity-temperature-depth tags (CTD, SMRU) were attached on the back of the

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head using Loctite™ 5-mintue epoxy. Data on the animal diving behavior and movements were collected by the SRDL, summarized, and transmitted via the ARGOS satellite system when the animal was at the surface. Tags recorded dive depth (min >5.5m), diving duration (min >10s), and surface interval, start and end time using a 4s sampling frequency. Additionally, four-hourly summaries of behavioral state were transmitted to build a comprehensive picture of dive behavior. Behavioral states included percentage time diving, swimming at the surface (<5.5m and 10s), hauled out resting, mean maximum depth, and dive duration. The start and end time of all haul-out periods was also recorded.

All data were stored in a transmission buffer for four days, before being deleted from tag memory (Fedak et al. 2001, Fedak et al. 2002). In the transmission buffer data were transmitted every 45 seconds when the tag broke the surface of the water and at 80ps intervals during the first five hours of each haul-out period. While the animal was in the water, surface swimming was recorded after no dives for six minutes. A haul out period began after the tag was dry for six minutes and ended after the tag was wet for 40 seconds. During haul-out periods the tags cycled 'on' for three hours, and 'off' for two hours with a maximum of 500 transmissions per day. Animal positions were calculated by the ARGOS satellite system (Argos 1996). Because all positions were time referenced, it was possible to determine approximate locations of all dives.

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Movement Analysis

Information from tags transmitted via the ARGOS system were integrated into Access databases, and exported into ArcGIS 9.0 (ESRI, Inc. Redlands, CA) and Matlab 7.1 (Mathworks, Inc. USA). Locations were screened by an iterative forward/backward averaging filter that identified and excluded locations that required transit rates greater than 4 ms^{-1} (Vincent et al. 2002). Dive positions were calculated using Argos positions based on a linear interpolation of time and distance and a swim speed filter (McConnell et al. 1992). Erroneous dive locations on land were filtered using the IKNOS toolbox (Y. Tremblay unpublished). Distance and course of travel during foraging trips were calculated in Matlab 7.1 using the great-circle distance and course between each dive location and summed for a trip. Speed across the surface (horizontal) was calculated between each position based on the great-circle distance between locations and the time elapsed (McConnell et al. 1992).

Trips from shore that contained dives were termed foraging trips, and used for subsequent analysis. Foraging trip duration was the time elapsed since a sea lions departure or end of period of rest on land, haul-out (end of HO), and its return to land (start of HO). Direction of travel during each foraging trip was determined by using the mode direction. The range of directions traveled between each dive position during a trip was estimated in Matlab 7.1 using the interquartile (IRQ; difference between the 75th and the 25th percentiles of the sample) range of directions. Because the distribution of directions during each leg of a trip was non-

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normal the IQR was used because it is a robust estimate of the spread of the data by eliminating changes or outliers in the upper and lower 25% of the data.

Foraging Behavior

To identify areas of high utilization, termed 'hotspots', we estimated distribution probability grids using kernel density analysis from the positions of all dives interpolated along the track of animals. Interpolated diving positions were used because they identify diving, and presumably, foraging behaviour; whereas, Argos positions merely indicated the presence of an animal at a given place and time but maybe independent of animals foraging activity. To examine the annual distribution of dive positions a kernel density distribution map was derived using the kernel density function in ArcGIS 9.0 (ESRI, Inc. Redlands, CA). Home ranges were compared between years using the minimum convex polygon feature in Hawth's Analysis Tools (3.24), an extension for ESRI's ArcGIS.

Activity Patterns

Activity patterns and diving frequencies were determined only from those days in which data were received for all 4 hour summary periods. Activity pattern data (percentage time hauled out, swimming or diving) were arcsine transformed prior to analysis to achieve normality. Start and end times for each haul out period were transformed to local time, and trip duration was calculated by subtracting end time of haul out period from start time of the next haul out period.

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Diet Data

Information on prey composition and temporal changes in diet of California sea lions was obtained through examination and identification of prey hard parts found in fecal samples collected at Año Nuevo Island (ANI; 37°6'N, 122°20'W). Diet of sea lions at ANI was assumed to be representative of the population in central California, including Monterey Bay because average estimates of swim speeds for sea lions for a 48-hour period encompass the region where tagging occurred (Fig. 1). Approximately 72% of all fish otoliths consumed were excreted in fecal samples within 48 hours during captive feeding trials (Orr & Harvey 2001). Further, ANI is the major population center for sea lions in central CA with approximately 75.4% of the population in central California occurred on the island (Weise 2000, Weise & Harvey In Review). Prey species were determined by identifying fish otoliths and cephalopod beaks recovered from fecal samples to the lowest taxon possible. Otoliths that could not be identified were excluded from the analysis because they could not be distinguished from prey already identified in the sample. Otoliths and cephalopod beaks were identified and enumerated using illustrations and pictures (Morrow 1979, Clarke 1986, Cannon 1987, Harvey et al. 2000), and an otolith reference collection at University of California Santa Cruz (Weise 2000) and Moss Landing Marine Laboratories (Harvey 1987). Prey hard parts were measured and species-specific correction factors were used to estimate standard length and mass of prey consumed (Orr & Harvey 2001). The contribution of each prey species to the

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diet for each year was expressed as a percentage of the total estimated mass (%M) of prey ingested (Weise & Harvey In Review).

Environmental Variables

Sea surface temperature (SST), chlorophyll-*a* and anomalies were used as an index of changes in the environment, and were created by acquiring nominally 1.1 km spatial resolution images from the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite for 2003 to 2005. The data were spatially projected onto a uniform grid, and temporally binned into 1-day and monthly composites. SST and chlorophyll-*a* values were then integrated over the coastal region where sea lion diving activity was greatest during 2003-04 based on kernel density analysis (36°N to 39°N and from the coast to 0.5° longitude offshore; Weise 2006) and temporally averaged to produce monthly mean values. Anomalies were then calculated by subtracting the climatological monthly mean for 2003 to 2005 from the same spatial region.

Analysis

Statistics were performed using Systat 11.0 (SPSS Inc. 2000) with a significance level of $p < 0.05$. Summary data are reported as mean ± SD, unless otherwise noted. Differences between means were tested among only adult males during both years using two-sample t-test or Mann-Whitney U-test, and relationships were tested using least-squares linear regression analysis.

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Results

Twenty-two sub-adult and adult male sea lions were tagged and tracked during 2003-04 for 19 to 127 days, and three adult males in 2004-05 for 91 to 118 days (Table 1). From 2003 to 2005 tags yielded 12,264 Argos positions of quality category Class 3 (12.9%), Class 2 (13.7%), Class 1 (15.3%), Class 0 (7.3%), Class A (21.1%), Class B (28.7%), Class Z (0.9%). There were a total of 1,282 tracking days covering 32,424 km with a mean number of 44 days and 1,098 km per individual during 2003-04 and 106 days and 3,120 km in 2004-05 (Table 1). There were 589 foraging trips during which diving occurred with a mean of 24 to 29 trips per individual lasting 0.9 to 2.6 days during 2003-04 and 2004-05, respectively.

Movement

In contrast to the northward male sea lion migration previously described (Mate 1975) and expected males tagged in Monterey dispersed along the entire coast of California and southern Oregon (Fig. 1). During 2003-04 the at-sea distribution and movements of male sea lions were confined to the continental shelf region as males dispersed along the California and southern Oregon coast; whereas, during 2004-05 two of three males made repeated trips up to 450km offshore. There was a positive relationship between distance traveled and duration of trips during both years, with longer trips having longer durations (2003-04, r^2=0.72, n=22, p<0.003; 2004-05, r^2=0.99, n=3, p=0.113; Fig. 2). Maximum trip distance was 820 km and maximum trip duration was 16 days, although not for the same trip. During the 2004-05 warm water anomaly mean trip distance was 124 km for an average of 2.4 days, which was

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significantly greater than 47 km for 0.8 days during 2003-04 (Table 1; Distance, Mann-Whitney, U=4.0, df=1, p=0.037; Duration, Mann-Whitney, U=0.0, df=1, p=0.008). Although the months that animals were tagged between years overlapped only during December and January, patterns in trip distance and duration were apparent. Trip distance and duration during 2003-04 differed little among months with a decreasing trend in SST anomaly, while there was a steady increase as the season progressed during 2004-05 with a marked increase in March that reflected a similar trend in SST anomaly (Fig. 3). Average transit rate was 2.5 km/hr (range 2.2 to 3.2 km/hr) and were similar between years (Mann-Whitney U=49.0, df=1, P=0.165).

Based on mode direction of travel among foraging trips indicated that males predominantly moved north (51%) during foraging trips, and they moved south with less frequency (14.5%; Figure 4a). There was considerable variation in direction within foraging trips, with 38% of foraging trips having an interquartile range in directions of 180°± 30° change, while only 27% of trips had 0°±30° change (Figure 4b).

Kernel density analysis was used to identify diving 'hotspots' or areas with the greatest density of diving activity. Kernel density plots indicate that there were four distinct areas of diving concentrations during 2003-04 including: around San Miguel Island (33.25°N, 119.45°W), within Monterey Bay and southward to Pt. Lobos (36.53°N, 121.97°W), offshore from Año Nuevo Island, and offshore from Cape Mendocino (40.44°N, 124.41°W; Fig. 5). There were apparent differences between

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2003-04 and the warm water year 2004-05 with foraging hotspots occurring in four distinct concentrations including: San Nicolas Island (33.24°N, 119.45°W), within Monterey Bay and southward to and offshore from Pt. Lobos, offshore from Half Moon Bay (37.51°N, 122.49°W) north to Pt. Reyes (37.95°N, 122.78°W), and several offshore sites. Home range based on minimum convex polygon analysis for males during the warm water year ranged from 781 km^2 to 2343km^2 (Table 1), and a mean range of 1451km^2 that was significantly greater than 2003-04 (213 km^2; Mann-Whitney U=0.0, df=1, p=0.006).

Activity and diving patterns

The primary difference in foraging behavior between years was in movement patterns and foraging effort, and to a lesser extent diving behavior. There was a significant difference in activity patterns between the warm water anomaly year (2004-05) and 2003-04 with a greater percentage of time surface swimming (Mann-Whitney U=5.0, df=1, p=0.044) and less time hauled out resting (Mann-Whitney U=36.0, df=1, p=0.049), although no difference in time spent diving was detected (Mann-Whitney U=26.0, df=1, p=0.528; Fig. 6). While all three activity patterns varied by month, the patterns were different between years. Although the proportion of time surface swimming did not vary greatly by month during 2003-04, there was a marked increase as the season progressed during 2004-05 that corresponded to increasing SST anomaly in contrast to a decreasing trend during 2003-04 (Fig. 7). Similarly, during 2003-04 the monthly percentage of time spent hauled out fluctuated up and down, while there was a decreasing trend throughout the season

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during the warm water anomaly of 2004-05 that corresponded to changing environmental conditions. Interestingly, the tradeoff in activity patterns between years did not change the time spent diving.

Consistent with the shallow continental shelf, mean dive depth for all male sea lions during 2003-04 was shallow (32±44m) and short duration (1.9±1.6 min). However, during longer trips further from shore in the warm water anomaly of 2004-05 males made deeper (46±10m, Mann-Whitney U=8.0, df=1, p=0.101) and greater duration dives (2.1±0.5 min; Mann-Whitney U=14.5, df=1, p=0.412) followed by significantly greater surface intervals (2.5±0.8min; Mann-Whitney U=4.5, df=1, p=0.036) than during 2003-04; Table 2). Seasonal trends in dive parameters were apparent with increases in dive duration and surface interval that reflected increasing SST anomaly as the season progressed during 2004-05, although little difference was observed in dive depth among months (Fig. 8). Consistent with a similar percentage of time spend diving while at sea, there was no difference in the frequency of dives between years (Mann-Whitney U=18.5, P=0.753; Table 2).

Sea lion diet

Approximately 1,249 fecal samples were recovered California sea lion haul-out sites on Año Nuevo Island, California from 2001 to 2005. Overall, 1,194 fecal samples (95.6 %) contained identifiable prey hard parts with 10,056 prey occurrences. Schooling prey were the predominant prey species based on reconstructed mass, including rockfish (*Sebastes* sp.; 38.4 %), Pacific hake

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(*Merluccius productus*; 16.3 %), Pacific sardine (*Sardinops sagax*; 14.2 %), market squid (*Loligo opalescens;* 10.4%), and northern anchovy (*Engraulis mordax*; 9.7 %).

Trends in the importance of prey species in the diet of California sea lions were apparent when comparing diet over multiple years. In addition to fecal samples collected during this study Figure 9 includes diet data collected in Monterey Bay from 1997 to 1999, which included the large 1997-98 El Niño event (Weise 2000, Weise and Harvey In Review). Although samples were collected at different locations than the present study, sites were within 2-day swimming range for sea lions at Año Nuevo Island (Fig. 1). Mean passage rate for greater than 70% of the otoliths recovered in fecal samples was 48 hours; therefore, species composition in fecal samples collected at ANI were assumed to be representative of this region. The decreasing trend in the importance of market squid, and the increasing trend of sardine in the diet from 2004 to 2005 during the warm water anomaly were similar to trends observed during the 1997-98 El Niño (Fig. 9). In contrast to the size of sardine during the increased importance in diet during the 1997-98 El Niño (Weise 2000), there was a large increase in juvenile size sardine in the diet, although adult sardine were still occurring at a rate similar to 2001 to 2004 (Fig 10). Interestingly, during 2004 to 2005 there was an increase in rockfish species in the diet in contrast to a decrease during the 1997-98 El Niño.

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Discussion

This study is the first to examine the at-sea movement and foraging behavior of male California sea lions, and demonstrates strong impacts of the warm water anomaly in 2005 on these behaviors. Despite the small sample size obtained during 2004-05, trends in movement patterns and foraging strategies were apparent and likely reflected the behavioral consequences of foraging during redistributed and reduced prey availability.

Ecological mechanisms underlying differences in movement and foraging strategies of male sea lions between years were founded in shifts in the distribution and abundance of prey species. During the warm water anomaly in 2005, the most spatially extensive and persistent sea surface temperature and primary productivity anomalies since the 1997-98 El Niño occurred within 100km of the coast (Thomas & Brickley In Review). Even greater anomalies occurred within the former foraging range of sea lions during 2003-04 along the coast 36°N to 39°N. Anomalies appeared because of the delayed onset of upwelling, which drives the productivity along the West Coast and creates the oceanographic features, such as frontal systems, shelf breaks, and thermal structure that help to create prey patches (Hunt 1990, Schneider 1991). Many prey species in the diet of sea lion lions are distributed relative to the thermocline (Morejohn et al. 1978, Vaughan & Recksiek 1978, Chess et al. 1988, Reynolds 2003, Helser et al. 2006, Hill K.T. et al. 2006), and would be redistributed with delayed onset of upwelling. During the anomaly in 2005, Brodeur et al. (In Review) found large disruptions in the trophic structure of the nektonic

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community off California that were greater than during El Niño conditions. Disruptions included the reduction and redistribution of forage fishes important in the foraging strategies and diet of marine predators. Previous shifts in distribution of pelagic schooling prey species in response to El Niño conditions have resulted in changes in sea lion diet (Lowry et al. 1990, Costa et al. 1991, DeLong et al. 1991, Lowry et al. 1991).

Declines in market squid and increases in sardine abundance during anomalous conditions off California during 2005 (Brodeur et al. In Review) were consistent with observed changes in sea lion diet, and likely explain altered foraging strategies. An expected southern shift in distribution of market squid during warm water conditions such as El Niño periods (Zeidberg 2006) was consistent with the absence of commercial catches in central California (Pacific Fisheries Information Network - PacFIN) and decreases in squid in sea lion diet. Size and abundance of squid decreases during El Niño conditions have been documented (Jackson & Domeier 2003, Zeidberg 2006), resulting in decreased fisheries landings and importance in the diet of sea lions (Lowry & Carretta 1999, Weise 2000, Weise & Harvey In Review). During El Niño and periods of warm water (Hill K.T. et al. 2006), and during 2005 there was a poleward displacement of southern offshore species to new geographic areas, including adult sardines that moved from Oregon to British Columbia and Southeast Alaska (Brodeur et al. In Review). This northward shift in sardine distribution was not only concurrent with increases in sardine in sea lion diet but similar to an increasing trend in sea lion diet during 1997-98 El Niño (Weise

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2000, Weise and Harvey In Review). In contrast to other years, however, the increasing importance of sardine in the diet during 2005 was based on the marked increase in juvenile rather than adult size sardine. Redistribution and changes in the abundances of sardine, squid, and rockfishes may explain the extensive offshore movements of male sea lions and their change in relative importance in the diet of sea lions during early 2005.

Behavioral responses of sea lions to changing oceanographic conditions and prey availability, theoretically, would include two possible modifications in foraging strategies: diving deeper in search of prey, or spending more time searching for prey at depth (Feldkamp et al. 1989). Although the physical oceanographic features in the CCS upwelling centers are temporally and spatially dynamic, marine predators likely have developed energy efficient foraging strategies to take advantage of predictable prey aggregations formed by frontal boundaries, current lines, and thermal structure. During 2005, delayed upwelling and ensuing warm water and decreased primary productivity resulted in significant alterations in the physical oceanography of the region (Schwing et al. In Review, Thomas and Brickley In Review) and consequently prey abundance and distribution (Brodeur et al. In Review). Male sea lions modified their foraging strategies in both of the predicted ways: by diving 27% deeper on average than during the previous year, and spending 10% greater period of time at depth per dive presumably searching for prey. A third modification of foraging behavior, however, documented during this study included covering greater distances at the surface in search of prey. Males spent 11% more of

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their time at sea swimming at the surface during foraging trips that were on average twice the distance and almost three times the duration as the previous year. Given the shallow diving depths of males in northern California (Weise Chapter 1), sea lions likely visually search for prey from the surface while swimming between patches similar to what has been described for fur seals (Boyd 1996), and minimize the greater transport costs associated with diving. Because SRDL tags do not collect a time-series data set we were unable to confirm bout feeding; however, bout feeding with surface swims in between has been described in this species (Feldkamp et al. 1989).

While there is often a spatial and temporal lag between changes in the physical environment and upper trophic level responses (Hindell et al. 1991, Costa 1993, Guinet et al. 2001, Bradshaw et al. 2002) changes in male sea lion foraging effort and diving patterns were apparent as the season progressed in 2004-05. Concurrent with changes in the integrated SST anomaly for the region, male foraging effort markedly changed as early as January 2005 with increased time swimming at sea searching during increasingly longer dives and greater subsequent surface intervals. Trip distance, although greater throughout 2004-05 than the previous year, did not increase until February into March 2005, and no change in trip duration was detected until March. Behavioral changes were consistent with the timing of the strongest recorded STT anomalies along the central California coast (35.75°N and 36.45°N) that began in February and lasted through May 2005 (Thomas and Brickley In Review).

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Many pinniped species are highly migratory covering thousands of miles in response to changing environmental conditions and breeding systems (Reidman 1990). Within otariids, individuals typically display an annual cycle of polygynous breeding and post-breeding dispersal, although in three species (California sea lion; northern fur seal, *Callorhinus ursinus*; and sub Antarctic fur seal, *Arctocephalus tropicalis*) it has been described as a migration (Mate 1975, Reidman 1990, Bowen & Siniff 1999). Male California sea lion migration has been described as uniform, with an orderly unidirectional movement northward throughout the extent of their range (Mate 1975). In contrast, our data indicated that male California sea lions dispersed during both years along much of the west Coast of the United States, traveling both north and south with animals often returning to breeding rookeries for brief periods of time during the non-breeding season before moving northward again. Migration is defined as persistent and more or less rectilinear movement, presumably between different parts of the home range, each with its own resources such as food or mates (Stern 2002). Male sea lion movement in this study was not rectilinear, the mode and interquartile range of movement during individual foraging trips indicated that animals moved in virtually all directions with the preponderance of effort constrained by the north/south coastline. Males rate of travel was greater than expected based on previous descriptions (Mate 1975), with individuals covering on average 50 to 58 km/day while at-sea throughout the period of tagging. Track data indicated that males visited numerous haul out sites along the California coast to rest, and made looping at-sea foraging trips to and from multiple resting sites.

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Previous descriptions of male sea lion migration may have been accurate (Mate 1975, Reidman 1990), but our research has indicated that males can move greater distances in a shorter period of time than previously known, and recent changes in the distribution and abundance of prey species, such as the return of large sardine (*Sardinops sagax*) schools off the West coast of North America (CalCOFI 1998), may not necessitate these previously large scale movements.

The degree to which male sea lions in this study dispersed along the coast following the breeding season was likely dependent upon fluctuations in environmental conditions and prey availability. During the first year, males foraged almost exclusively over the continental shelf during relatively short trips; whereas during the second year males still dispersed along the coast but incorporated offshore excursions into their foraging strategies. Over the course of ten to eleven days during February and March 2005 male #28599 looped offshore three times from central California to the Channel Island and back traveling 760 km to 820km for each trip. A second male #28588 made repeated loops offshore from the Monterey Bay region and back traveling 480km to 800km over the course of seven to 16 days. Males during 2003-04 did make a few trips along the coast in the range of 400km, but the trips were three to four days in duration and linked to movements to and from breeding rookeries. For example, male #37590 traveled 426km in three days from Año Nuevo Island southward to San Miguel Island during November 2003. Male #44640 traveled 474 km from San Nicolas Island to Pt. Lobos over the course of three and a half days. The greater duration of trips given the distance

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during 2004-05 compared to 2003-04 indicates that males invested more time searching for prey patches rather than simply transits. Offshore excursions during 2004-05 have not previously been described for this species, and appear to be consistent with the presence of positive coastal warm water anomalies and negative primary productivity along central California (Fig. 1).

Responses of pinniped foraging behavior to fluctuation in environmental conditions have been well studied in a few species, including adult female California sea lions (Costa et al. 1989, Trillmich et al. 1991). During the 1982-83 El Niño adult female California sea lions, which are central place foragers, exhibited greater variability in the time away from pups than during non-El Niño years, being absent from pups a mean of 9.2 days compared to 2 to 4.5 days during non-El Niño conditions (Heath et al. 1991). Further, females dove deeper and longer during El Niño conditions than non-El Niño conditions. In contrast to males, however, females spend an increased percentage of time diving and decreased time swimming. This difference between males and females is related to differences in reproductive roles and parental care. Male foraging behavior is not constrained by dependent young on rookery sites because they provide no parental care and extended their search area by swimming over greater distances. Whereas females constrained to foraging close to rookery sites worked harder to locate prey by diving a greater percentage of their time while at-sea during longer and deeper dives in close proximity to rookery sites (Feldkamp et al. 1989).

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Behavioral comparisons with other male otariids were limited to a few species with mostly movement and tracking data (Green 1997, Hindell & Pemberton 1997, Boyd et al. 1998, Campagna et al. 2001, Kirkwood RJ et al. 2002, Page et al. 2005), one study that included dive data (Page et al. 2005), and no studies investigating male behavioral response to environmental fluctuations. Satellite tracking of two males South American sea lions (*Otaria flavescens)* indicated that trips were 5.7 days in duration with a mean distance of 591 km, and maximum distances of 862km and 875km (Campagna et al. 2001). These males remained over the continental shelf restricting their diving depth to an estimated range of 50 to 100m. New Zealand sea lions (*Phocarctos hookeri)* males were bleach marked and observed at various breeding rookeries (Robertson et al. 2006). Depending on which of two estimates of swim speed were used, trip durations were 2 to 6.7 days or 6.5 to 22.4 days over distances of 580 to 930 km. Among fur seals, male Australian fur seal (*Arctocephalus pusillus doriferus*) trips lasted 8 days covering 200 to 400 km from colonies traveling over the continental shelf between southern Australia and Tasmania (Kirkwood et al. 2002). Page et al. (2005) reported that New Zealand fur seal (*A. forsteri*) foraging trips lasted 9 days with diving to mean depths of 52.1 m for 3.6 min. Two Antarctic fur seal (*A. gazella*) males traveled close to 900km while transiting from South Georgia toward the South Orkney Islands with estimated dive depths of less than 100m (Boyd et al. 1998). Free-ranging adult male northern fur seals (*Callorhinus ursinus*) have been described as moving off shelf and further north in the Pacific than adult females (Loughlin et al. 1999). Juvenile male northern

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fur seals made off shelf excursions similar to adult females lasting 9 to 30 day and covering 171 to 681 km. Fur seals dive deeper over shelf area but had a shallow overall mean diving depth of 17.5 m for 1.2 min (Sterling & Ream 2004). Although differences in trip duration and distance were apparent in California sea lion between 2003-04 and 2004-05, longer trips during the warm water anomaly were similar what has been observed in other adult male otariids.

Although the origin of the anomaly in 2005 was unprecedented, similar events like El Niño occur regularly throughout the lifetime of long-lived male sea lions. Increased time spent foraging observed in male sea lions during the anomaly in 2005 is a strategy that links foraging behavior with reproductive and life history strategies. Dispersal from breeding rookeries and extended periods at sea foraging are key components to a life history strategy that is free of parental constraints and maximizes the ability of animals to accrue resources for breeding. This pattern coupled with the inherent physiological benefits bestowed upon males with larger body size (lower mass-specific metabolic rate, increase aerobic dive capacity) likely buffer them from these short term fluctuations in prey availability unlike smaller females or younger age classes of sea lions. However, changes in distribution and abundance of small forage species utilized by seabirds and marine mammals may be amplified over multiple years affecting the short and long-term trophic structure of coastal ecosystems (Brodeur et al. In Review). This study highlights value of interannual studies, the plastic response of an apex predator to bottom-up climatic

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forcing, and the utility of apex predators as sentinels of climatic variability and change.

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Table 1. Summary information on male California sea lions outfitted with Sea Mammal Research Unit SRDL tags. Means (±SD) and maximum for trip distance and duration for animals tagged in Monterey, California during 2003-04 and 2004-05.

Animal ID	Age Class	Tracking Days	Total Travel Distance (km)	Number of Trips	Mean Trip Distance (km)	Maximum Trip Distance (km)	Mean Trip Duration (days)	Maximum Trip Duration (days)	Minimum Convex Polygon (km^2)
2003 / 04									
28587	Adult	47	976	37	26.4 ± 4.3	180	0.5 ± 0.1	1.4	217
28588	Subadult	49	1277	36	36.5 ± 5.9	181	0.7 ± 0.1	2.6	213
28589	Subadult	63	1291	27	47.8 ± 9.2	202	1.4 ± 0.3	4.9	234
28590	Adult	24	654	9	72.7 ± 24.2	225	1.2 ± 0.4	2.0	363
37588	Subadult	29	550	19	28.9 ± 6.6	94	0.7 ± 0.2	1.6	17
37589	Subadult	23	359	28	13.3 ± 2.6	43	0.3 ± 0.1	0.9	16
37590	Subadult	39	1403	12	116.9 ± 33.8	426	1.8 ± 0.5	3.9	245
37591	Adult	127	1956	56	36.2 ± 4.9	130	0.7 ± 0.1	2.8	171
37592	Adult	77	1947	39	49.9 ± 8.0	289	0.8 ± 0.1	2.9	225
37593	Adult	31	627	9	69.7 ± 23.2	139	1.1 ± 0.4	2.2	23
37597	Subadult	33	440	21	23.2 ± 4.6	87	0.6 ± 0.1	1.8	14
37598	Adult	19	302	17	18.9 ± 4.3	65	0.4 ± 0.1	0.6	19
44632	Adult	44	1248	17	78.0 ± 19.5	321	1.1 ± 0.3	2.9	252
44633	Adult	31	522	9	58.0 ± 19.3	184	1.0 ± 0.3	3.4	45
44634	Adult	43	1225	29	29.0 ± 7.9	242	0.7 ± 0.1	2.4	277
44635	Adult	32	1423	24	61.9 ± 12.1	331	0.8 ± 0.2	2.9	229
44636	Adult	37	1376	25	55.1 ± 11.0	221	0.6 ± 0.1	1.8	601
44637	Adult	38	881	22	41.9 ± 8.5	195	0.7± 0.1	2.2	103
44638	Adult	37	1178	14	84.2 ± 22.5	420	1.0 ± 0.3	3.0	611
44639	Adult	37	503	12	41.9 ± 12.1	210	1.0 ± 0.3	2.6	157
44640	Subadult	79	2925	40	77.0 ± 11.6	474	1.1 ± 0.2	3.7	450
mean		**44 ± 2.4**	**1098 ± 140**	**24 ± 3**	**47.4 ± 7.8**	**222 ± 26**	**0.8 ± 0.1**	**2.5 ± 0.2**	**213 ± 178**
2004 / 05									
26343	Adult	91	1424	23	64.7 ± 13.8	331	1.7 ± 0.4	5.7	781
28588	Adult	118	3976	49	90.4 ± 13.6	783	1.8 ± 0.3	16.0	1229
28599	Adult	108	3961	15	264.0 ± 68.2	820	4.2 ± 1.1	11.2	2343
mean		**106 ± 14.0**	**3120 ± 848**	**29 ± 10**	**124.2 ± 20.4**	**644 ± 157**	**2.4 ± 0.3**	**11.0 ± 3.0**	**1451 ± 804**

Table 2. Mean diving parameters and effort for 22 male California sea lions tagged during 2003-04 and 3 sea lions during 2004-05 (Weise Chapter 1). Values are mean ± standard deviation.

Year	Number Animals	Dive Depth (m)	Dive Duration (min)	Surface Interval (min)	Dive Frequency (# dives/4 hr)	Swim Speed (m/s)
2003 / 04	22	33 ± 37	1.9 ± 0.6	1.5 ± 0.9	27.9 ± 8.1	0.74 ± 0.11
2004 / 05	3	46 ± 10	2.1 ± 0.5	2.5 ± 0.8	27.3 ± 7.1	0.62 ± 0.13

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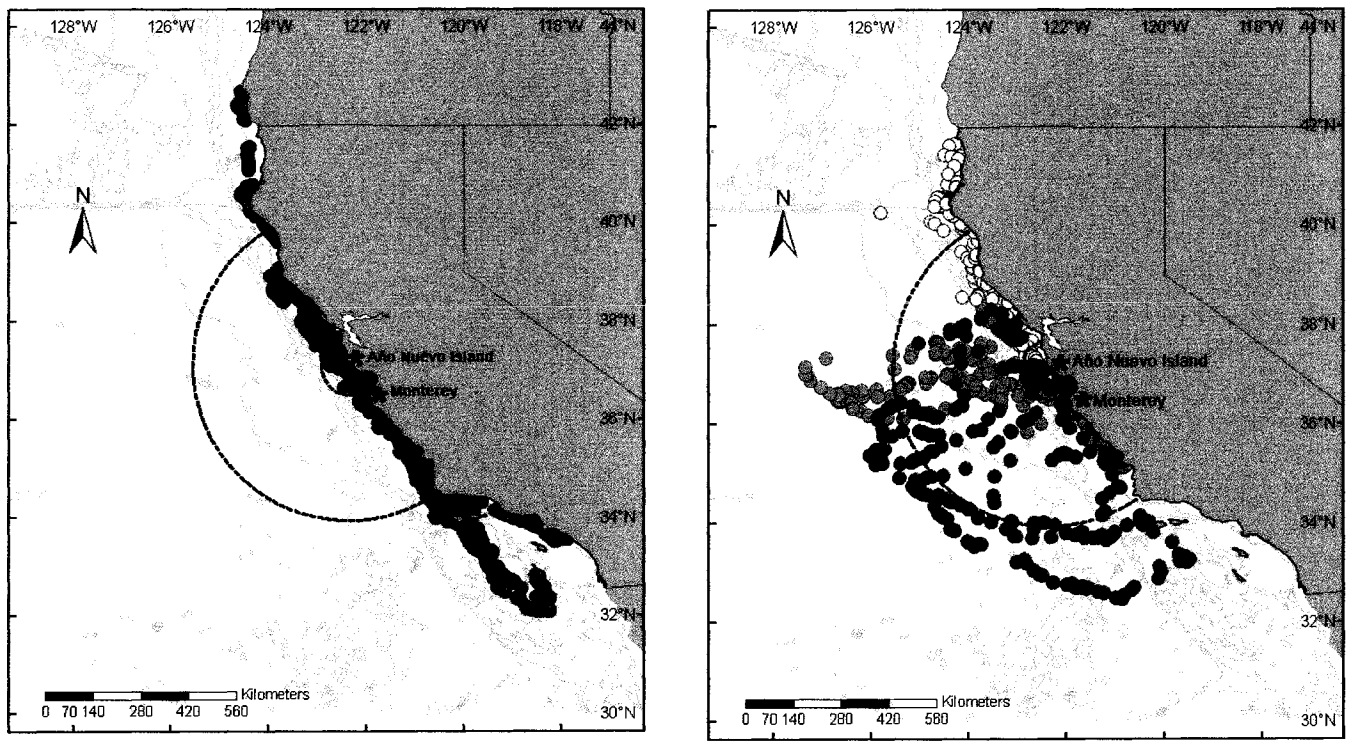

Figure 1. Interpolated at-sea diving positions for a) 22 male California sea lions tagged in Monterey California during 2003-04; and b) 3 adult male sea lions during 2004-05. Stars indicate tagging location in Monterey, and site for fecal sample collection at Año Nuevo Island. Inner circle indicates the distance sea lions can travel in 48 hours at their estimated mean rate of travel (0.77 m/s) and outer circle is the distance traveled at their maximum recorded speed (4.11 m/s) as a representation of the area of inference for diet analysis based on the mean passage rate of 48 hours for otoliths recovered in fecal samples (Orr and Harvey 2001).

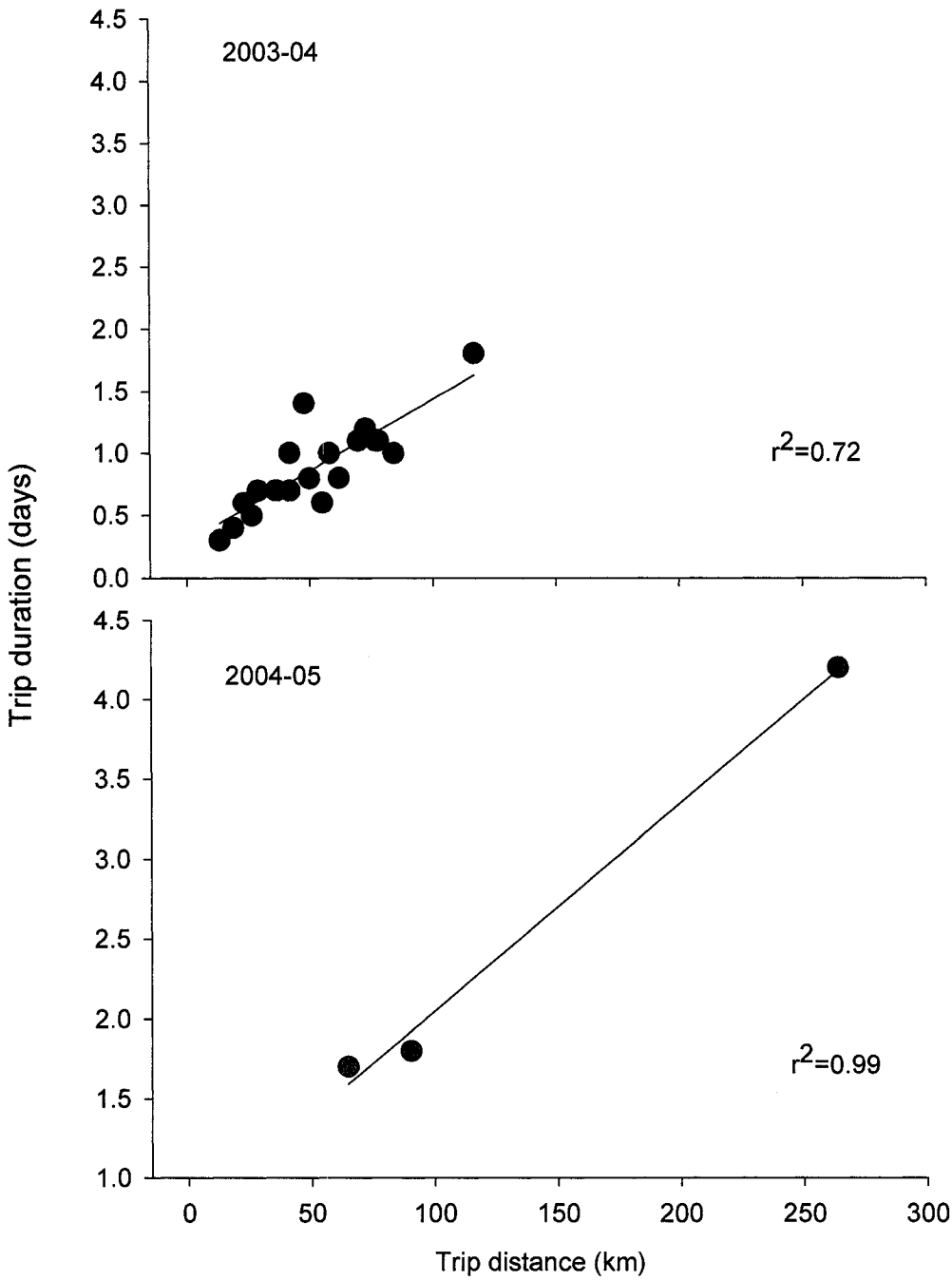

Figure 2. The relationship between mean trip distance and duration for individual male California sea lions tagged during a) 2003-04 (dark blue) and b) 2004-05 (light blue).

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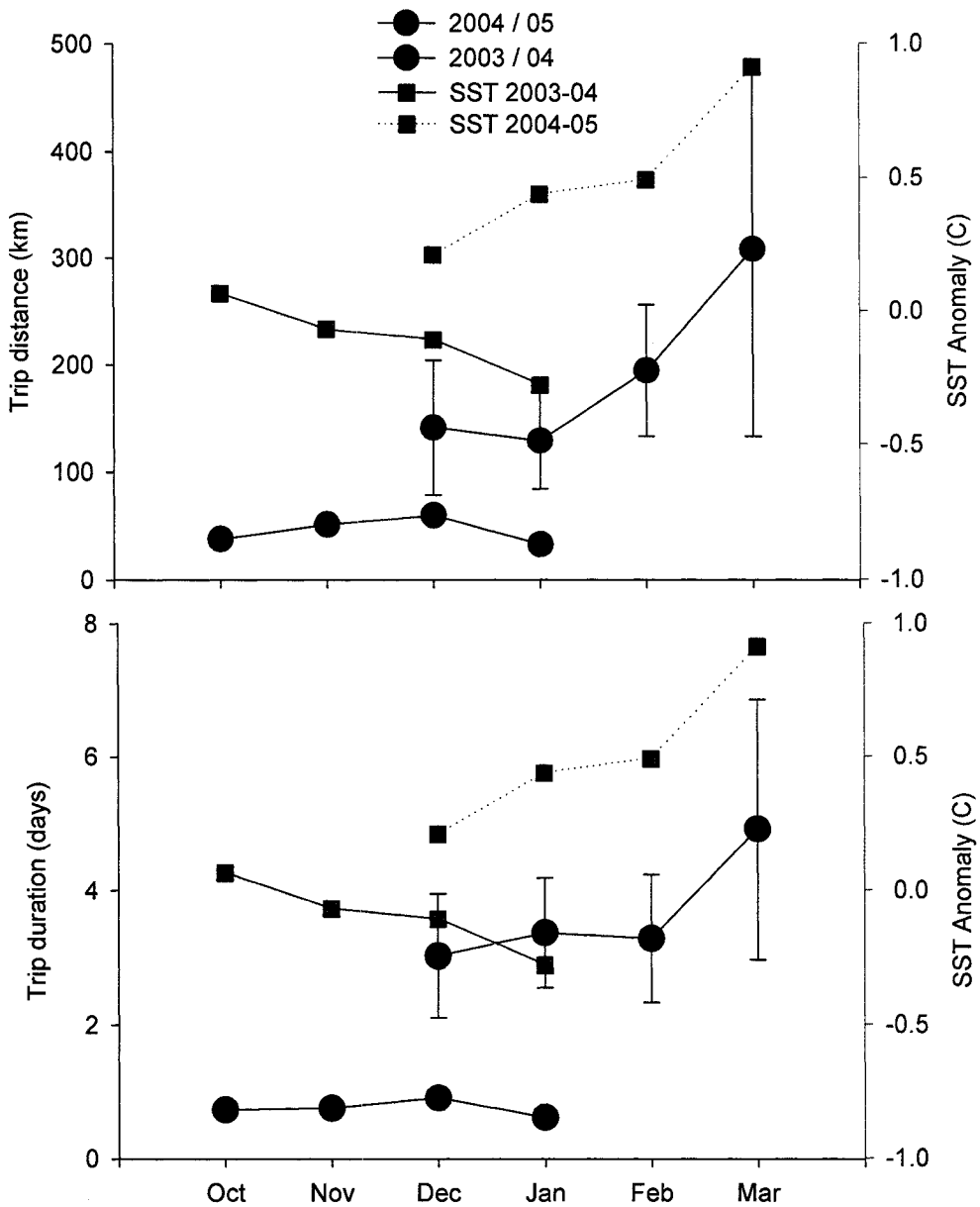

Figure 3. Monthly a) trip distance and b) trip duration for male sea lions tagged during 2003-04 and 2004-05. Red line indicates the monthly integrated SST anomaly for the region sea lions dispersed (36° N-39° N, offshore 0.5°).

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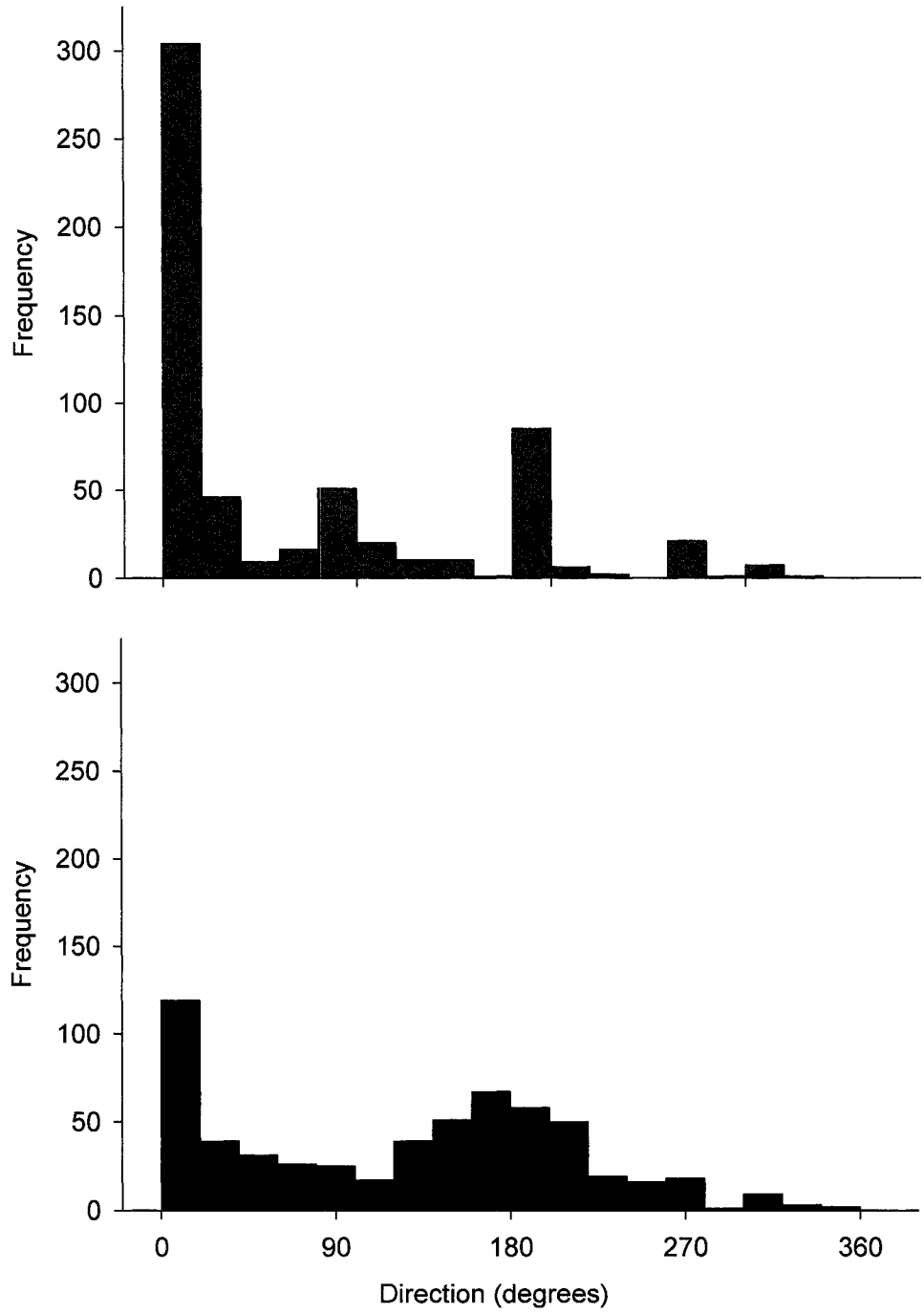

Figure 4. a) Mode direction of travel among all sea lion foraging trips during 2003-04 and 2004-05 (light blue), and b) interquartile range of travel direction within foraging trips (dark blue).

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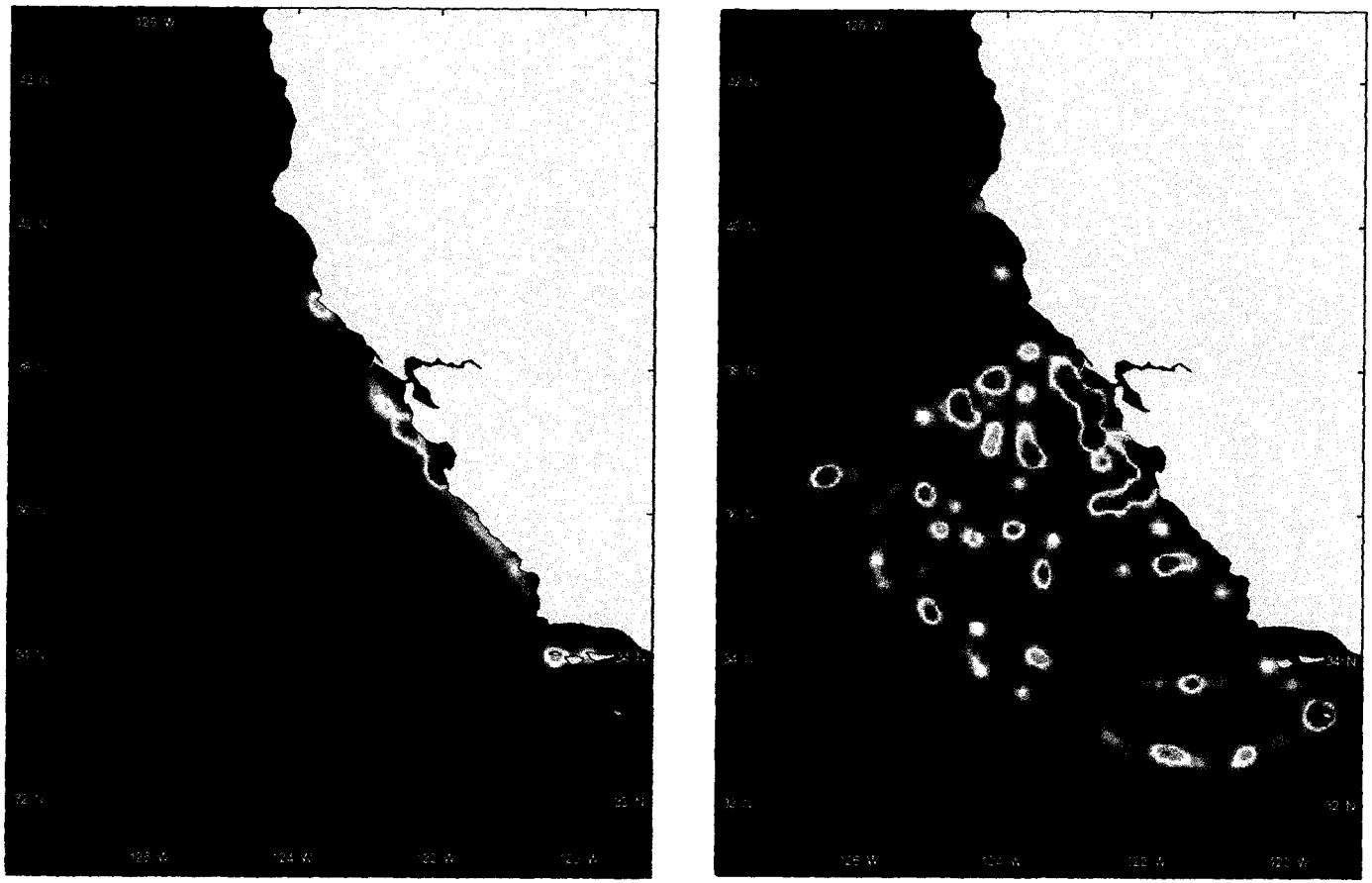

Figure 5. Kernel density analysis (density plot) of dive positions for a) 22 adult and subadult male sea lions tagged during 2003-04 and b) three adult male sea lions tagged from 2004-05. Red and orange colors indicate greater density of dive effort and light blue is less dense dive effort.

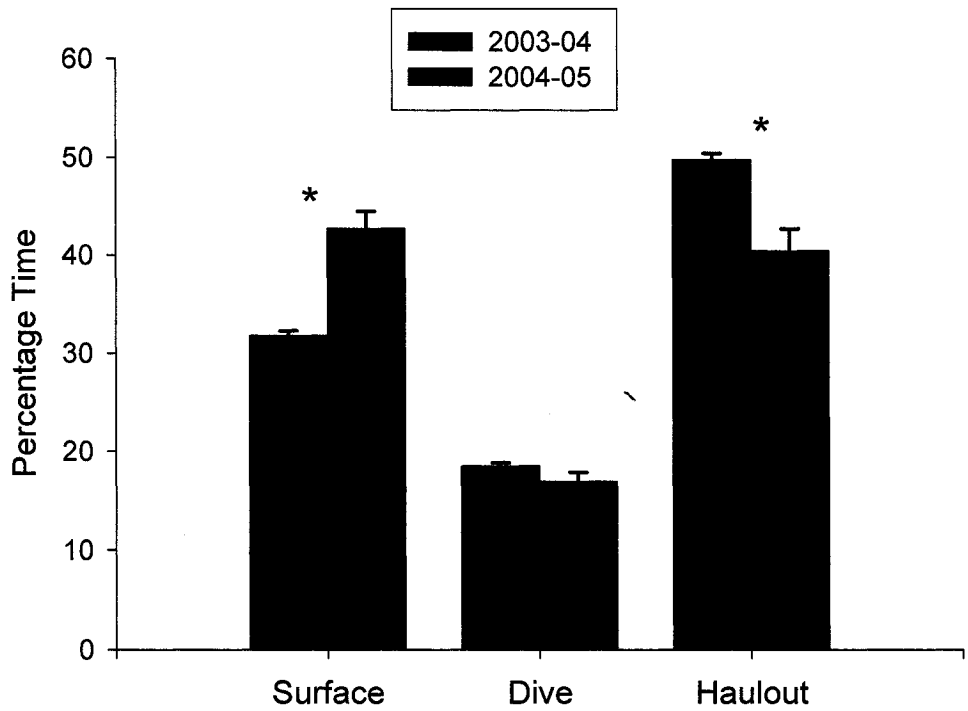

Figure 6. Annual comparison of percentage time spent surface swimming at sea, diving at sea, and hauled out on land resting. Asterisks indicate a significant difference between years.

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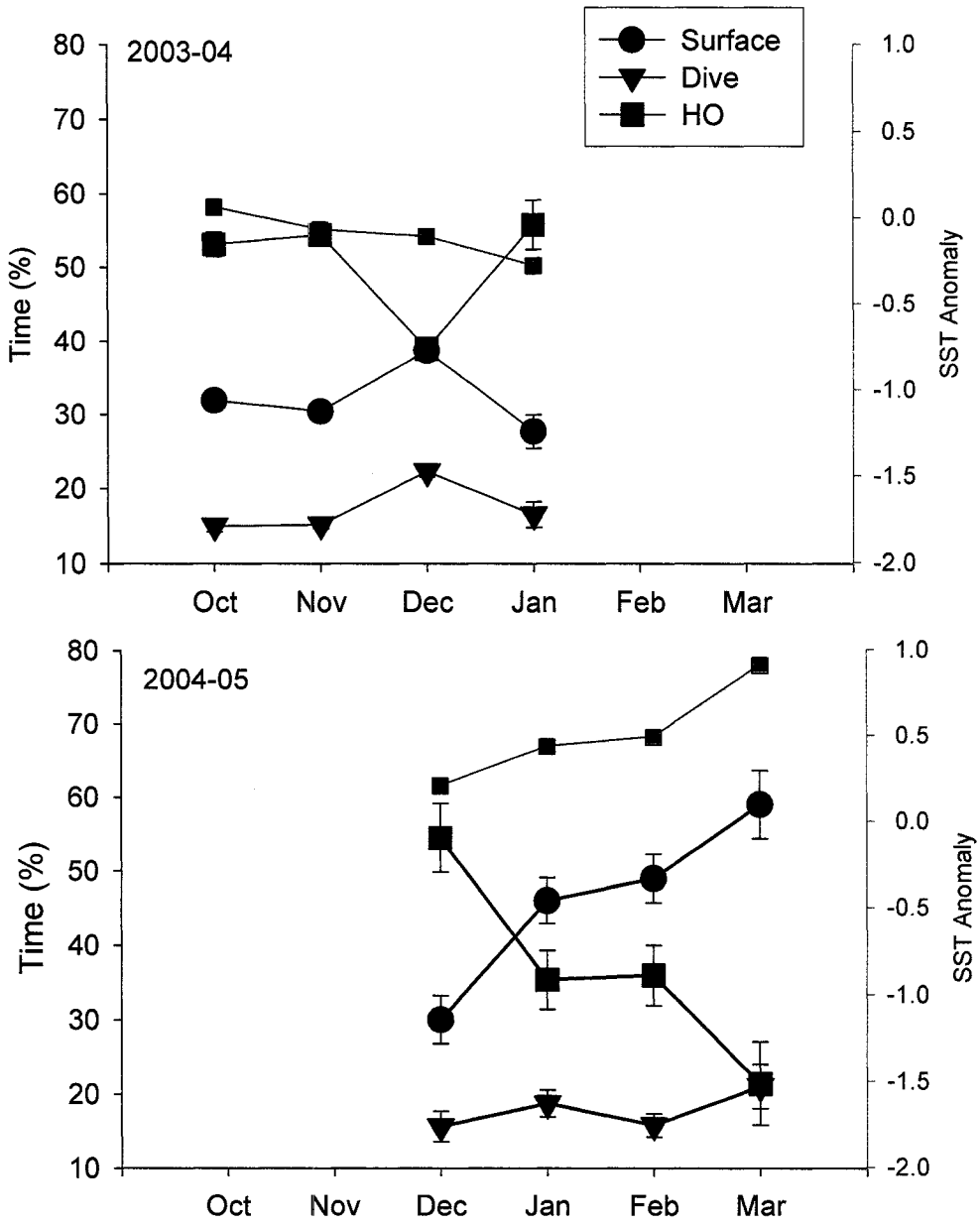

Figure 7. Monthly trends in the percentage time spent surface swimming at sea, diving at sea, and hauled out on land resting during a) 2003-04 and b) 2004-05. Red line indicates the monthly integrated SST anomaly for the region sea lions traveled (36° N-39° N, offshore 0.5°).

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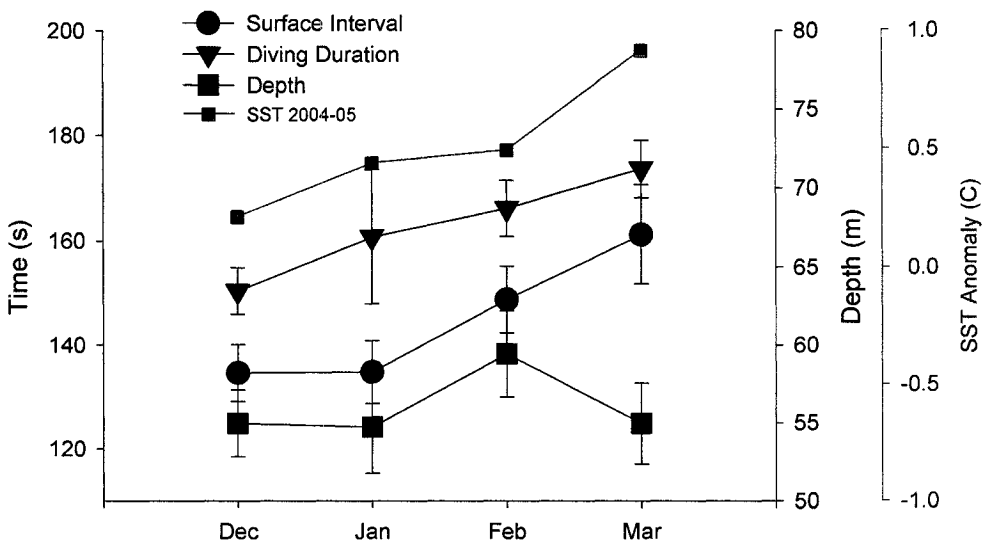

Figure 8. Monthly trends in dive depth and duration, and surface intervals between dives for California sea lions tagged during 2004-05. Red line indicates the monthly integrated SST anomaly for the region sea lions traveled (36° N-39° N, offshore 0.5°).

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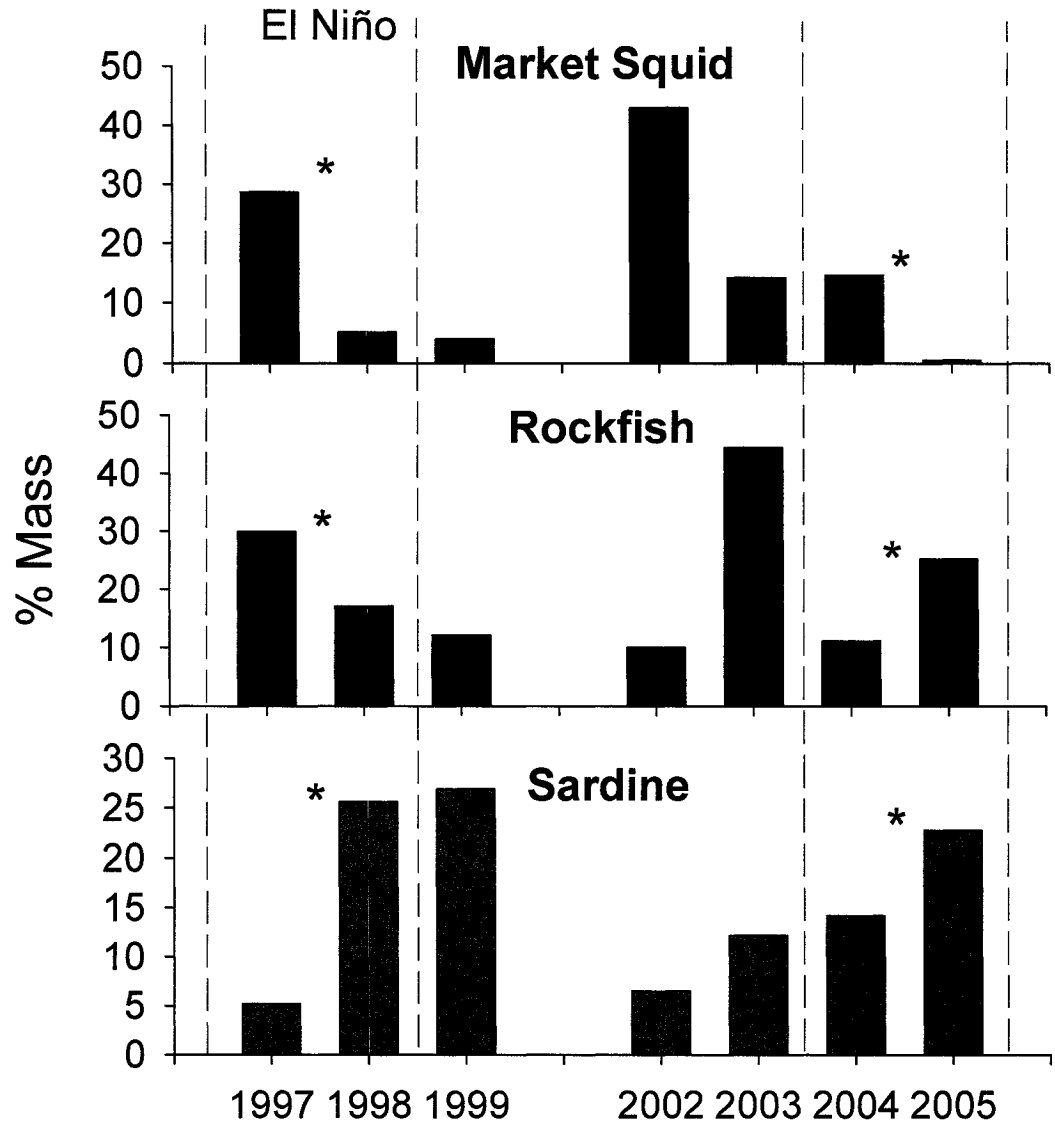

Figure 9. Percentage mass for sardine, rockfishes, and market squid identified and reconstructed from sea lion fecal samples collected on Año Nuevo Island from 2002 to 2005, and fecal samples collected by Weise and Harvey (In Review) in the Monterey Bay from 1997 to 1999.

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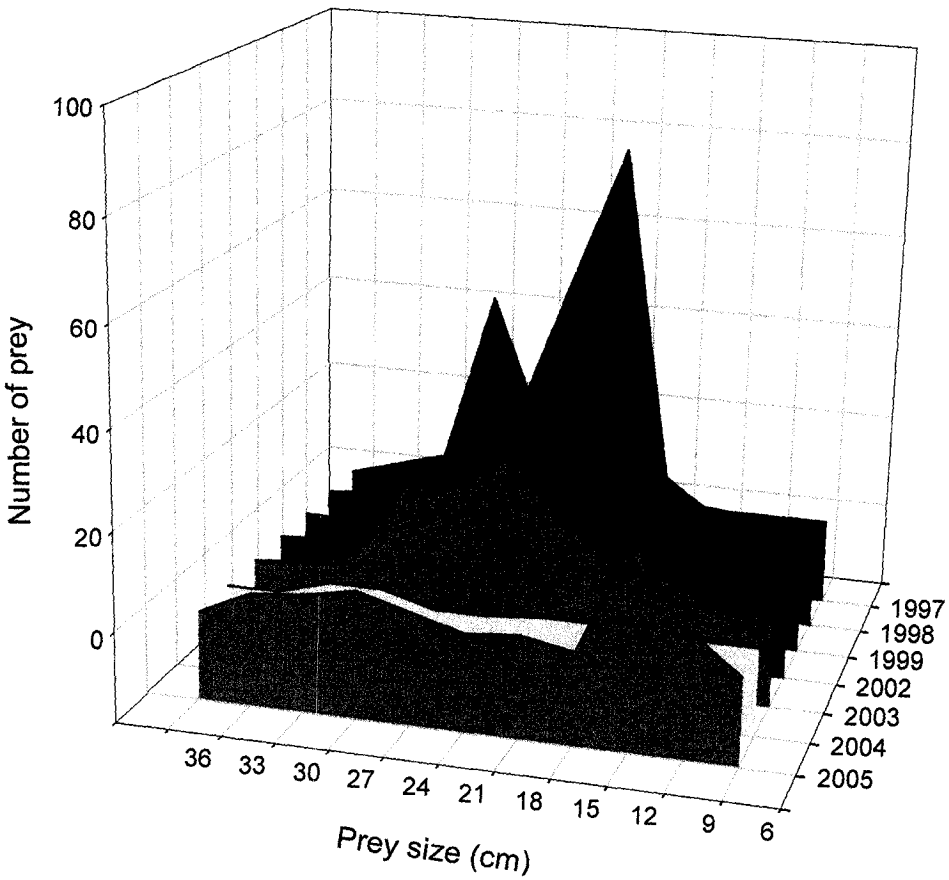

Figure 10. Reconstructed body length of sardines identified in fecal samples of California sea lions collected on Año Nuevo Island during 2002 to 2005, and sea lion fecal samples collected in Monterey Bay from 1997 to 1999 (Weise 2000, Weise and Harvey In Review).

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Chapter 3. Pysiological Diving Capacity of California Sea Lion (*Zalophus californianus*) Across Sex and Age Classes

Introduction

For air-breathing vertebrates, an individuals ability to acquire food resources in the marine environment results from the interaction between an animals behavior and physiological capability, both of which may vary by age, body size, and gender. Development of oxygen storage capacity is particularly important for marine mammals and birds that rely on large onboard stores for diving and foraging activity during and following their transition to nutritional independence. Although blood typically accounts for more than 50% of the total oxygen reserves of adult pinnipeds (Kooyman 1985), previous studies indicated that neotates and juveniles had significantly less oxygen stores in their blood than adults (Thorson & LeBoeuf 1994, Horning & Trillmich 1997, Costa et al. 1998, Burns 1999, Ponganis et al. 1999b, Noren et al. 2001, Noren et al. 2002, Richmond 2004, Noren et al. 2005, Fowler et al. In Review). In addition to lower blood oxygen stores, previous researchers have found that myoglobin was a key oxygen store in the muscle of marine mammals, and took the longest to develop of all oxygen storage parameters (Thorson 1993, Richmond 2004, Fowler et al. In Review)

Sexual dimorphism is evident among marine mammals and physiological diving capacity, maximum diving depths, and dive durations exhibit an allometric relationship with body size (Schreer & Kovacs 1997, Halsey et al. 2006). Furthermore, the requirement for greater energy intake and increased diving capacity

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with size may lead to different foraging strategies and differences in ecology between the sexes. Although differences between male and female foraging behaviors of sexually dimorphic marine mammals has been examined (northern elephant seal, *Mirounga augustriostris*, Le Boeuf et al. 2000); southern elephant seal, *M. leonine*, Slip et al. 1994; grey seal, *Halichoerus grypus*, Beck et al. 2003; New Zealand fur seal, *Arctocehpalus forsteri,* Page et al. 2005), little is known about differences between sexes in the physiological diving capacity.

In pinnipeds, studies on neonates revealed that pups, like most young terrestrial mammals, had disproportionately greater metabolic rates, limited control of heart rate and metabolic processes. For many species the implications of these physiological limitations on the diving and foraging ability of young pinnipeds has not been considered (Elsner et al. 1977, Rea & Costa 1992, Blackwell & Le Boeuf 1993, Castellini et al. 1994). Recently, studies of the development of blood oxygen storage capacity indicated that the rate at which pups mature is closely tied to the length of the dependency period (Thorson & LeBoeuf 1994, Horning & Trillmich 1997, Merrick & Loughlin 1997, Costa et al. 1998). In most true seals (Family Phocidae), nursing is a short period (4 to 50 days) and weaning is abrupt when the females abandon pups on the beach and return to sea to forage (Costa et al. 1991). In contrast, sea lions and fur seals (Family Otariidae) nursing lasts between 6 months and three years, with the females making short foraging trips lasting 3 to 7 days (Costa et al. 1991).

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In general, otariids store proportionally more oxygen in their muscles than phocids, so the development of myoglobin stores could particularly constrain the diving behavior of young sea lions (Kooyman 1989). Because otariid pups begin to dive well before weaning and the prolonged development of muscle oxygen stores, the full development of blood oxygen stores prior to weaning is expected. Noren et al. (2001) found that postnatal development of myoglobin oxygen stores was independent of the length of the dependency period. Further, myoglobin content increased significantly during subsequent development, which likely corresponds to increased activity levels, thermal demands, and time spent in apnea during swimming and diving.

Although a plethora of information is available on the oxygen stores of many pinniped species, few researchers have simultaneously measured the development of blood and muscle oxygen stores in otariids (Steller sea lion, *Eumatopias jubatus*: Richmond 2004; Australian sea lion, *Neophoca cinerea*: Fowler et al, In Review), and to date no research has included all age classes and both sexes through adulthood in the analysis. Limited data are available on the oxygen stores of California sea lions (*Zalophus californianus*; Ponganis et al. 1997, Kuhn et al. 2006), and no data are available on differences between the sexes or the development of oxygen stores, and their affect on diving capacity in this species.

California sea lion is sexually dimorphic with adult males greater than four times adult female size. Female sea lions give birth at island rookeries in southern California from late May through late June each year and remain in the area of

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breeding rookeries throughout lactation until weaning at six to 11 months (Melin 1995). California sea lion pups are not precocial when born and do not enter the water for several weeks after birth, and may not begin foraging until seven months of age at the earliest (Boness 1991). Following the breeding season, most sub-adult and adult males disperse northward to central and northern California (Weise 2006, Chapter 2), and possibly as far as Oregon, and Washington (Bartholomew 1967, Mate 1975), whereas females remain on the rookery with their pups. Here we examine the effects of body size, age, and sex on blood and muscle oxygen stores in sea lion pups through adults and evaluate how differences in oxygen stores may affect diving capacity and foraging behavior.

Methods

Field sites and data collection

A total of 31 adult male, 25 adult females, 16 sub-adult males, 28 juveniles, 5 nine-month old pups, and 11 five-month old pups were captured during this study. Adult and sub-adult male California sea lions were captured in the municipal harbor of Monterey, California (36°36.5' N, 121°53.4'W) during September through December 2003 and 2004 using a modified aluminum enclosure (3m x 4m x 2m) and squeeze cage (2.5m x 1m x 1.5m; DeLong pers. comm.). The enclosure was situated on a floating platform (4m x 8m) and secured to the United States Coast Guard wharf near the base of the rock jetty where animals normally haul out on land to rest. Captures involved the voluntary entry of sea lions into the enclosure

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followed by the manual triggering of a sliding type door to enclose the animals inside. Animals were transferred to the squeeze cage where they were physically restrained and if necessary sedated with Midazolam intramuscularly at 0.20mg/kg (mixed with atropine at 0.02 mg/kg) in conjunction with isoflurane gas (0.5 to 2.5% w/O_2) or with isoflurane alone.

Adult females and juveniles were captured on Año Nuevo Island (37°6'N, 122°20'W) during September through October 2002, and adult females, juveniles, and pups were captured on San Nicolas Island (32°16.0'N, 119°29.8'W) during late October 2003 and 2004, and March 2005. Animals were selected based on healthy appearance, accessibility with minimal disruption to the rookery, alertness and proximity to other alert individuals. Adult females, juveniles, and pups were captured with a modified hoop net (Fuhrman Diversified, Seabrook, TX, USA). The nets were a soft mesh with a hole at the end for the animal's nose to facilitate breathing. Once in the net animals were transferred to a kennel for holding and, if necessary, given an intramuscular dose of Midazolam (0.20mg/kg mixed with atropine at 0.02 mg/kg). Isoflurane gas was administered with oxygen via a portable vaporizer (Gales & Mattlin 1998). Lengths and girths were measured on all animals, including adult and sub-adult males, at six locations along the long axis of an animal and each animal was weighed (Dyna-Link MSI–7200).

Age of pups, juvenile, and sub-adult males was assessed using date of capture, body morphometrics, and degree of canine tooth eruption. We were unable to verify the specific age in years for any size class, and young animals were broken into two

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categories based on size. Adult males were distinguished from sub-adult males by size and presence of a sagital crest. Adult females were distinguished from juveniles by size and presence of lactation.

Blood and muscle sample collection

Blood samples were collected from the caudal gluteal vein, interdigital rear flipper vein, or jugular vein. For a subset of animals of each size class an initial blood sample to measure hematocrit (Hct) was collected before the induction of isoflurane gas because of the decline of Hct as the spleen contracts following isoflurane delivery (Zapol et al. 1989, Castellini et al. 1996, Costa et al. 1998). Following isoflurane induction and full sedation of animals a blood sample (time, T = 0) was taken and placed in a heparin Vacutainer (BD Vacutainer SST, Franklin Lakes, NJ, USA). Each animal received an intra-venous injection of Evan's Blue dye at a dose of 0.6 mg kg^{-1} and a concentration of 10, 20, or 30 mg mL^{-1} to determine blood volume (El-Sayed et al. 1995). Sequential 8 to 10 ml samples were taken as described above at approximately time (T) = 10, 20, and 30 minutes post injection. Syringes were weighed with a portable field balance (±0.001 g) before and after injections to accurately determine the mass of dye injected. Upon completion of injections, but before removal of the needle, blood was drawn into the syringes to flush the contents of the syringe into the vein insuring that all dye was injected. Blood samples were stored on ice until transported to the lab, centrifuged, and stored at -20°C until analysis.

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Muscle biopsies of approximately 50 mg each were collected from live animals during anesthesia by making a 2 to 3 cm incision through the blubber layer then using a 6mm canula or a biopsy needle. The biopsy site was cleaned with sterile wipes before and after the procedure. Biopsies were collected from the dorsal triceps complex and supraspinatus located above the scapula, which are primary locomotor or swimming muscles in otariids. Muscle samples were stored on ice until transported to the lab and stored at -80°C until analysis.

Laboratory analysis

Complete blood counts (CBCs) were determined for juvenile, sub-adult male, adult male and female sea lions collected in 2003 in the Monterey Harbor and Año Nuevo Island using an Animal Blood Counter (ABX Diagnostics, France), located at the Marine Mammal Center in Sausalito, California. This Animal Blood Counter was calibrated for California sea lion blood analysis and programmed for the size and shape of their red blood cells. Red blood cell (RBC), hemoglobin (Hb) concentration, hematocrit (Hct), and mean corpuscular hemoglobin concentration (MCHC) were determined for each animal. Castellini et al. (1996) reported that Hct values measured using automated Coulter counters were 4% to 15% greater than values obtained from microcentrifugation. To investigate the accuracy of our method, we determined Hct for a subset of sea lions using standard clinical microhematocrit centrifugation and compared estimates based on Coulter counter methods on the same individuals. No difference in Hct ($F_{1,24}$=0.009, P=0.926) was found between the two methods.

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Hematocrit using microcentrifugation and hemoglobin using the methanocyanide technique was measured on all animals sampled in the Monterey Harbor in 2004, and San Nicolas Island during 2003 and 2004. Upon returning from the field, 10 *ul* aliquots of whole blood from T=0 heparinized tubes were added to test tubes containing 2.5 ml of Drabkins Reagent (Ricca Chemical Co., Arlington, TX, USA). Samples were read at 540 nm on a split-beam spectrophotometer (Spectronic 1001, Bausch and Lomb, Rochester, NY, USA), and Hb was calculated using a linear regression based on absorbance values from a series of standards (Fisher Scientific, Pittsburgh, PA, USA).

Remaining blood samples collected at 0, 10, 20, and 30 minutes were centrifuged at 3,000 x g for 15 min, within four hours of being collected to separate blood cells from plasma. Supernatant containing blood plasma was frozen and stored at -20°C. Maximum absorption of the Evan's Blue dye in sea lion plasma using a spectrophotometer was determined to be 624 nm. Photometric absorbance values were determined at 624 and 740 nm for all plasma samples. As 740 nm does not absorb blue, these values were used to calculate the blank optical density at 624 nm to account for possible hemolysis and precipitate (Foldager & Blomqvist 1991). Serially collected Evan's Blue samples were logarithmically transformed and fit to a regression line, and the instantaneous dilution volume was determined from the y-intercept (El-Sayad et al. 1995). Blood volume (BV) was calculated from the hematocrit and plasma volume (PV= mg dye injected / dye concentration; Swan & Nelson 1971) as follows:

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$$BV = PV / [(100 - Hct) / 100]$$

Myoglobin content (g Mb (100 g wet muscle)$^{-1}$) was determined for all animals using the procedure of (Reynafarje 1963).

For all sea lions sampled in the Monterey Harbor in 2004, and San Nicolas Island 2003 and 2004 we estimated the average MCHC using the following equation:

$$MCHC = (Hb / Hct) * 100$$

Total available oxygen stores were calculated for each sea lion using the methods of Davis & Kanatous (1999) and Costa et al. (2001) as follows:

$$\text{Arterial blood oxygen (ml)} = BV * 0.33 * B_{BO2} * 0.80$$

$$\text{Venous blood oxygen (ml)} = BV * 0.67 * B_{BO2} * S_{VO2}$$

where BV = blood volume (ml), 0.33 = percentage of arterial blood, 0.66 = percentage venous blood, B_{BO2} = capacitance coefficient of blood (g Hb l^{-1} * 1.34ml O_2 g^{-1} Hb), where Hb oxygen carrying capacity of 1.34 ml O_2 (g^{-1}) was assumed (Kooyman 1989), and S_{VO2} = oxygen saturation of mixed venous blood (% = [(B_{BO2} – 50)/ B_{BO2}] x 100), which assumes an oxygen content that was 5% by volume less than the initial arterial blood oxygen. We assumed that the arterial blood was 100% saturated at the beginning of the dive as a result of predive hyperventilation (Kooyman et al. 1980; Ponganis et al. 1993), but only 80% was available with the

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other 20% used to maintain vital body and brain functions. Total muscle oxygen stores were calculated as follows:

$$\text{Skeletal muscle oxygen (ml)} = BM * 0.37 * Mb * 1.34$$

where BM = body mass (kg), 0.37 was the fraction of muscle mass in the body (Ponganis et al. 1997), Mb was myoglobin concentration, and 1.34 O_2 g^{-1}= oxygen binding capacity of myoglobin (Kooyman 1989). Muscle oxygen content was based on complete depletion of the 100% saturated Mb and the assumption that myoglobin was uniformly distributed throughout the musculature. Diving lung oxygen stores were calculated using the following:

$$\text{Lung oxygen} = (55 \text{ ml } O_2 \text{ kg}^{-1} * BM * 0.15\ FO_2)$$

where 55 ml O_2 kg^{-1} was the measured diving lung volume of the closely related Steller sea lion (Lenfant et al. 1970), BM = body mass, and 0.15 FO_2 was the oxygen extracted from the air in the lungs (Kooyman et al. 1971).

Statistics

Size and age class of sea lions were defined using a hierarchical cluster analysis to detect discontinuous groupings or 'clumps' of data points. Euclidean distance and an average linkage function were used as this measure maximized the cophenetic correlation coefficient and thus best represented the raw data structure (Gauch 1982, McGarigal et al. 2000; Table 1). Change in oxygen stores with body size and during the development of California sea lions was examined using a one-

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way ANOVA followed by a Tukey pairwise comparison test to compare inter-age differences in blood oxygen storage parameters (Hct, Hb, MCHC, PV, BV), muscle oxygen stores (Mb), absolute and mass-specific total oxygen stores (blood and muscle). Sex differences in the blood and muscle oxygen store parameters were analyzed using t-tests in size classes containing both sexes (5-month old pups, small juveniles, and adults). ANCOVA was used to compare differences in the rate (slope) of development between sexes, based on least-squares regression, of myoglobin, and blood, muscle, and total mass-specific oxygen stores. All variables were tested for normality and homogeneity of variances. Statistical analysis was completed using SYSTAT 11.0 software package. Means were reported ± standard error. Values were considered significant if $P \leq 0.05$.

Results

Age and size related changes in blood and muscle oxygen stores

There were significant size and age related changes in blood oxygen stores of Hb ($F_{6,127}$=15.644, P<0.001), Hct ($F_{6,68}$=33.034, P<0.001), and MCHC ($F_{6,116}$=2.203, P=0.048; Fig. 1). The most pronounced changes in Hct, Hb, and MCHC occurred in pups between 5 and 9 months of age; however, a slight decrease in MCHC from 5 to 9 month old pups occurred followed by an increase from juveniles (39 to 70kg) to adults. There was an increase in the number of red blood cells during early development, whereas the oxygen carrying capacity of individual red blood cells decreased early before increasing to relatively stable levels.

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Mass-specific PV ($F_{6,106}$=7.977, P<0.001) and BV ($F_{6,106}$=12.507, P<0.001; Fig. 2a) had a slight decrease from 5 to 9-month old pups before increasing significantly through large juveniles to adult size. In contrast, absolute PV ($F_{6,106}$=190.604, P<0.001) and BV ($F_{6,106}$=192.570, P<0.001; Fig. 2b) did not significantly increase until large juveniles size (70kg) with a linear increase with increasing size to subadult males (125kg) and again to adult males (175kg). Muscle myoglobin increased significantly ($F_{6,91}$=48.013, P<0.001) from pups (21 to 23kg) to juvenile and sub-adult stages (39 to 125kg), and from the sub-adult size to adults (Fig. 3).

As a result of ontogenetic changes in blood and muscle oxygen stores, total blood ($F_{6,91}$=124.127, P<0.001), muscle ($F_{6,91}$=157.481, P<0.001), and total oxygen storage capacity ($F_{6,91}$=213.616, P<0.001) significantly increased throughout development (Fig. 4). Additionally, the site of primary oxygen storage shifted from the blood towards the muscles as body size increased. Mass-specific blood ($F_{6,91}$=20.036, P<0.001), muscle ($F_{6,91}$=48.026, P<0.001), and total oxygen stores ($F_{6,91}$=35.172, P<0.001) changed significantly with increasing size (Table 2).

Sex differences in oxygen stores

Differences in the development of some blood oxygen store parameters and absolute and mass-specific blood, muscle, and total oxygen stores among size classes resulted from differences between sexes. No significant differences in Hct and Hb were found between sexes for any age class; however, MCHC was significantly greater in adult males than adult females ($F_{1,62}$=4.565, P=0.037) indicting a greater capacity for red blood cells of males to carry oxygen than

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females. Absolute PV was not significantly different until adulthood ($F_{1,62}$=4.565, P=0.037); whereas, absolute BV in males was greater than females beginning in large juveniles (39kg; $F_{1,14}$=4.790, P=0.046) and continuing through adult sizes ($F_{1,52}$=395.067, P<0.001), which tracks the size differences between sexes in this species. Muscle myoglobin was not significantly different between the sexes until adulthood ($F_{1,41}$=81.001, P<0.001); however, the rate (slope) of development of Mb stores was significantly different between the sexes (t=4.93, P<0.001; Fig. 5).

Total blood and muscle oxygen stores, and total oxygen stores were significantly greater in males than females beginning with the small juvenile age class (blood: $F_{1,14}$=4.319, P=0.047; muscle: $F_{1,14}$=6.212, P=0.026; total: $F_{1,14}$=5.242, P=0.038; Fig. 5) continuing through adulthood (blood: $F_{1,41}$=142.122, P<0.000; muscle: $F_{1,41}$=75.419, P<0.000; total: $F_{1,14}$=202.189, P<0.000). Differences in absolute PV, BV, and blood, muscle, and total oxygen stores between sexes were not surprising given that males are significantly greater in body size than adult females. Sex differences in oxygen stores as a consequence of body size became evident while animals were small juveniles, although differences in mass were not statistically significant at this age.

Unexpected differences occurred between sexes when comparing mass-specific blood, muscle, and total oxygen stores. Adult males had a greater absolute amount of oxygen in their blood and muscle stores than adult females due to greater body mass. However, when differences in mass were accounted for female mass-specific muscle oxygen stores were significantly greater than adult males ($F_{1,41}$=81.413,

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P<0.001; Table 2), although mass-specific blood oxygen stores were not different ($F_{1,41}$=0.521, P=0.475). Similarly, the rate (slope) of development of male mass-specific blood oxygen stores was no different than females (t=-0.37, P=0.714; Fig. 6a), whereas, the rate of development of female mass-specific muscle oxygen stores was significantly greater than males (t=4.47, P<0.001; Fig. 6b). Greater mass-specific muscle oxygen stores in females resulted from greater myoglobin content coupled with smaller body size. Although mass-specific oxygen stores of females were significantly greater than those of males ($F_{1,41}$=202.189, P<0.001), the rate of development in females was not significantly greater than males (t=1.43, P=0.155; Fig. 6c).

Discussion

Our findings demonstrate pronounced differences in blood and muscle oxygen stores of California sea lions as a function of size, age, and sex. The most prominent findings included how long it took for blood and muscle (4 to 6 years) oxygen stores to develop. In fact, sea lions were foraging independently well before oxygen stores reach adult levels. Although a difference in Mb between sexes might be expected given the sexual dimorphism in this species, this is the first study in marine mammals to report adult female myoglobin concentrations in their muscles that were greater than adult males. Further, greater Mb levels gave adult females greater total mass-specific oxygen stores compared to adult males.

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Effects of age and body size on oxygen stores

Blood oxygen stores were not fully developed at weaning and differences among size classes were related to age and body size. Among the blood parameters, only hematocrit had reached adult levels when pups were weaned at around 9-months old. Differences in absolute plasma and blood volume and consequently blood and total oxygen stores were not surprising given the differences in body size among age/size classes. While there appeared to be no limit in red blood cell production and only a limited delay in Hb early in development, the lack of increase in mass-specific blood volume until juveniles were larger (70kg) was unexpected and perhaps related to the inability of blood oxygen store development to surpass growth rate.

Similar to our results, Australian sea lion at the onset of independent foraging had oxygen stores lower than adult values (Fowler et al. In Review). This is in contrast to what was found in Steller sea lions, (Richmond 2004) and Galapagos fur seals, (*Arctocephalus galapagoensis*, Horning and Trillmach 1997) where juveniles had reached adult levels at weaning. Horning and Trillmich (1997) found that Hct, Hb, and RBC in yearling Galapagos fur seals were similar to adult values; however, blood volume was not measured so a direct comparison of blood oxygen stores was not possible.

Although the development of blood oxygen stores was delayed past weaning in some otariids, it has been suggested that the development of Hct and Hb corresponds to lactation intervals (Richmond 2004). For example, longer lactating species, such

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as Australian sea lion and Galapagos fur seal, do not reach adult levels of Hct and Hb until 18 months (Fowler et al. In Review) and 15 months of age (Trillmich 1992), respectively. Whereas, species with shorter lactation intervals had adult levels of Hct and Hb at weaning, including Steller sea lions (Hct: 5 months; Hb: 9 months; (Richmond 2004) and California sea lions in the southern Gulf of California (Hct and Hb: 9 months; Kuhn et al. 2006). In this study, however, California sea lions do not follow this pattern because they are weaned between seven and 11 months of age and did not have adult levels of Hct and Hb until they were small juveniles with an estimated age of 1.5 to 2.5 years. Mean blood volume (105.0 ml kg^{-1}) for small juvenile sea lions was similar to a value (96.0 ml kg^{-1}) for juvenile California sea lions reported by (Ponganis et al. 1997). Although young animals do not have the blood oxygen storage capacity of adults, the amount of oxygen they do have has been closely linked to the amount of time a young animal can spend underwater foraging (Costa 1993).

Our results support the prediction that myoglobin concentration would not be fully developed until adulthood as seen in seabirds (Weber et al. 1974, Haggblom et al. 1988, Ponganis et al. 1999a), cetaceans (Dolar et al. 1998), and pinnipeds (Lenfant et al. 1970, Thorson and LeBoeuf 1994, Richmond 2004, Burns et al. 2005). Development of Mb was likely reflective of major developmental milestones in the ontogeny of total body oxygen stores and diving behavior. The first significant change in Mb during development was between 9-month old pups and small juveniles, which corresponded to animals' shift to foraging independently. Pups at

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weaning (9-month old) had approximately 60.7 % of adult myoglobin content and small juveniles had 73.7% of adult values. Mean Mb levels (3.0 g%) and muscle oxygen stores (520.1 ml O_2) in small juveniles were consistent with previously published values for juvenile California sea lions (mass: 40 kg; Mb: 2.8 g%; Muscle O_2 stores: 505 to 631 ml O_2, Ponganis et al. 1997).

Within pinnipeds, there appears to be a marked difference in the required period of postnatal development of Mb between phocids and otariids. Thorson (1993) and Kohin (1998) found that 300-day old elephant seals returned from their first trip to sea with 100% of adult Mb levels, and Burns et al. (2005) indicated that harbor seal yearlings in Alaska and California had similar Mb concentrations as adults. Sub-adult males in this study (estimated age 4 to 6 years), however, had Mb concentrations only 83% of adult values. Although total mass-specific oxygen stores of sub-adult males were not significantly different than adult males, their mass-specific muscle oxygen stores and consequently their cADL were significantly less than adult males (Table 2). Determining the driving force in differences between phocids and otariids ontogeny of diving capacity is confounded by differences in lactation strategies. While otariids pups are provisioned by females for prolonged periods (months) of time resulting in a decreased necessity to forage independently early in life, phocids are weaned within weeks of birth and required to forage independently. Therefore, these differences may be due to greater exposure to hypoxic conditions during the development of oxygen stores in phocids compared to less exposure to hypoxia in otariids during extended maternal provisioning.

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Total body oxygen stores at the transition to independent foraging (9-month pups) were 54% of adult values, and male sea lions did not reach the equivalent of adult levels until the sub-adult stage (4 to 6 years). The magnitude of this difference between juveniles and adult females was consistent with California sea lions on the island of Los Islotes, in the southern Gulf of California that had 59% of adult stores (Kuhn et al. 2006), and similar to related species such as Steller sea lion pups that had 80% of adult females (Richmond 2004), Australian sea lion pups that had 50% of adult female values (Fowler et al. In Review), and juvenile New Zealand sea lions that had 87% of adult stores (Costa et al. 1998).

Differences between sexes in diving capacity

While differences in Mb between sexes have been observed in pinnipeds (Richmond 2004), it was unexpected that adult female Mb concentrations, mass-specific muscle and total oxygen stores would be greater than adult males. Similar to Steller sea lions (Richmond 2004), these differences were not apparent in younger age classes. Differentially greater Mb levels in adult females were consistent with other research that suggested that Mb and muscle oxygen stores are malleable (Morrison 1966, Stephenson et al. 1989, Macarthur 1990, Noren et al.2001). Further, changes in only muscle oxygen stores and not blood oxygen stores in adult female sea lions indicated that blood stores may be at their developmental capacity and only muscle stores that are malleable once sexually maturity is reached.

Different Mb levels between the sexes of sexually dimorphic species has been suggested to be related to different foraging or diving strategies as might be

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expected with significant differences in body size. Metabolic rate scales to body mass$^{0.75}$, whereas oxygen storage capacity scales to the body mass$^{1.0}$ (Kooyman 1989). All things being equal, therefore, large adult male sea lions should be able to dive for greater duration and deeper than smaller adult females based simply on body size. Greater exposure to increasing periods of apnea during diving resulting in increased Mb levels may explain how adult females extend their physiological diving capacity to compensate for the smaller body size. Conversely, less exposure to periods of apnea during shorter duration dives in adult males may explain lower Mb levels. Males may not be approaching their physiological capacity, and therefore, avoid incurring the energetic costs associated with developing muscle oxygen stores, yet were meeting their energetic demands using the advantage of greater body size. Further support for this hypothesis was found in sex differences in mass-specific total oxygen stores (blood and muscle combined), which were greater in adult female sea lions than in males corresponding to observed differences in patterns of diving in adult female and male California sea lions.

Aerobic dive limit

To evaluate California sea lion physiological diving capacity relative to their diving behavior I calculated their aerobic dive limit (cADL) for different size classes and sexes of animals. The cADL was determined by dividing the total amount of oxygen available during diving (this study) by estimates of metabolic rate (MR) from the literature. Ponganis et al. (1997) measured the ADL of a juvenile California sea lion, the only measurement to date in an otariid, although MR was not measured

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or estimated. Post-submersion increases in lactate occurred following dives of 2.3 min duration. Costa (1991) measured a field MR of 22 ml O_2 min^{-1} kg^{-1} for adult female sea lions with an estimated cADL of 1.8 to 2.0 min, and Feldkamp (1987) and Williams (1999) measured a surface swimming MR of 12 ml O_2 min^{-1} kg^{-1} yielding a cADL of 3 to 3.5 minutes in juvenile animals. Based on this MR data a post-submersion increase in lactate at 2.3 min for a juvenile animal was equivalent to a diving MR of 17.8 ml O_2 min^{-1} kg^{-1}.

For adult animals, field MR measured by Costa et al. (1991) over estimated diving MR because it averaged time spent at the surface and time spent diving. We assumed that the relationship between resting MR (6.6 ml O_2 min^{-1} kg^{-1}, Feldkamp 1987; 5.1 ml O_2 min^{-1} kg^{-1}, Butler et al. 1992) and diving MR (17.8 ml O_2 min^{-1} kg^{1}, Ponganis et al. 1997) for juvenile sea lions was constant across age classes. Therefore, adult diving metabolic rate was scaled relative to body mass based on 40 kg juvenile (44.83 ml O_2 min^{-1} $kg^{0.75}$). If the resting MR measured by Hurley and Costa (2001) for adult males was 6.43 ml O_2 min^{-1} kg^{-1} (mean mass 128 kg) and adult females was 10.23 ml O_2 min^{-1} kg^{-1} (mean mass of 66 kg) then the estimated diving metabolic rates were:

Adult Male Diving Metabolic Rate = 52.1 ml O_2 min^{-1} $kg^{0.75}$ * $BM^{0.75}$/ BM

Adult Female Diving Metabolic Rate = 59.7 ml O_2 min^{-1} $kg^{0.75}$ * $BM^{0.75}$/ BM

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California sea lions demonstrate a hypometabolic response that is proportional to the duration of submersion that was at or exceeded the standard or resting MR, indicating that the aerobic MR decreases with increasing breath-hold duration (Hurley & Costa 2001). A point estimate of cADL, therefore, does not take this into account and does not reflect the true range of their aerobic capacity. To encompass this range an upper limit of cADL was estimated using the resting MR, and the lower limit using the estimated diving MR was used.

Significant differences among all estimates of cADL for different age classes of sea lions were reflective of major milestones in the development of total body oxygen stores ($F_{6,90}$=68.48, P<0.001). The first major change in cADL occurred between pup and juvenile stage when animals begin foraging independently and corresponded with increased Hb and Hct. The second change among cADLs estimates occurred between juveniles and adults, which was consistent with the final stage of Mb development.

Aerobic diving capacity of juvenile California sea lions ranged from 48.5% to 56.7% of adult male diving capacity and 64.0% to 85.7% of adult female capacity at the transition to independent foraging (Table 3). During the next three to five years, at least in males, cADL increased to 69.7% to 85.1% of adult capacity paralleling the development of total oxygen stores. This delay in cADL is not surprising given the delayed development of blood (2.5 to 3.5 years) and to a greater extent muscle oxygen stores (4 to 6 years), triggering a transition from a greater reliance upon blood oxygen stores to muscle oxygen stores.

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The minimum cADL determined for adult female and male sea lions in this study was consistent with mean dive duration of free-ranging adult females of 1.5 to 2.8 minutes (Feldkamp et al. 1987), and 2.1 minutes (Kuhn 2006), and adult males with 1.9 min to 2.3 min mean dive duration (Weise 2006, Chapter 1).

Summary

This study confirms that blood and muscle storage parameters are not developed by the end of the dependency period, which is consistent with the ontogeny of oxygen stores found in a diverse array of cetaceans, phocids, and otariids. It took approximately 1.5 to 2.5 years for blood parameters to reach adult levels, and it was not until animals were an estimated 2.5 to 3.5 years of age before mass-specific blood volume reached adults concentrations. Although our findings were consistent with other marine endotherms (pinnipeds, penguins, and cetaceans) that require a period of postnatal development for Mb concentrations, sea lions were particularly delayed with sub-adult animals (4 to 5 years old) with Mb concentrations only 83% of adult values. This indicates there may be a fundamental difference in the physiological development of muscle in otariids compared with phocids. Regardless, immature sea lions have reduced physiological capacity until the age of four to six years. These limitations may help to explain the greater mortality of juvenile California sea lions during environmental perturbations and limited prey availability associated with El Nino events (DeLong et al. 1991). Differences in adult sea lion myoglobin concentrations and mass-specific muscle and total oxygen stores, and differences in oxygen stores among size classes was the

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basis for differences in aerobic diving capacity and likely different foraging strategies among different size, age, and sex sea lions.

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Table 1. Mean (± SE) morphometric measurements used to determine different age classes of California sea lions.

Age Class	Mass (kg)	Standard Length (cm)	Curvilinear Length (cm)	Anterior Foreflipper (cm)	Canine* (mm)	Incisor* (mm)
5-month pups	20.9 ± 1.4	100.2 ± 1.4	105.2 ± 1.4	31.0 ± 0.6	n/a	n/a
9-month pups	23.2 ± 1.2	100.4 ± 1.7	105.4 ± 1.7	29.6 ± 0.7	3.7 ± 0.5	6.5 ± 0.3
Small juvenile	39.1 ± 1.6	126.4 ± 2.5	129.0 ± 3.2	37.3 ± 0.7	8.3 ± 0.7	8.6 ± 0.4
Large juvenile	70.1 ± 2.7	156.4 ± 2.0	163.9 ± 2.6	47.4 ± 0.8	n/a	n/a
Sub-adult male	125.4 ± 3.8	187.5 ± 2.0	197.1 ± 1.9	54.8 ± 0.5	n/a	n/a
Adult male	175.0 ± 7.8	205.6 ± 2.3	216.2 ± 2.3	58.8 ± 0.6	n/a	n/a
Adult female	86.7 ± 2.1	165.4 ± 2.0	173.2 ± 2.2	48.2 ± 0.7	n/a	n/a

n/a - not available

* Data from 9 month old pups and small juveniles captured on San Nicolas Island in March 2005.

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Table 2. Mean body mass, mass-specific oxygen store parameters (blood, muscle, and total), and calculated minimum and maximum aerobic dive limits (cADL) based on diving metabolic rate (MR) and resting metabolic rate (MR) for different size classes of free-ranging California sea lions. Values are mean ± standard error.

		Mass – specific Oxygen Stores			Min cADL[a]	Max cADL[b]
Size Class	Mass (kg)	Blood O_2 (ml kg^{-1})	Muscle O_2 (ml kg^{-1})	Total O_2 (ml kg^{-1})	Diving MR	Resting MR
5-month pup	20.9 ± 1.4	9.4 ± 0.8	11.1 ± 0.7	28.7 ± 1.4	1.6 ± 0.2	4.4 ± 0.2
9-month pup	23.2 ± 1.5	8.3 ± 0.7	11.3 ± 1.9	27.8 ± 1.6	1.6 ± 0.1	4.2 ± 0.2
Small juvenile	38.9 ± 3.0	17.7 ± 0.7	13.8 ± 0.4	39.8 ± 1.1	2.2 ± 0.1	6.0 ± 0.2
Large juvenile	75.7 ± 3.4	18.2 ± 1.4	14.5 ± 0.4	41.0 ± 1.4	2.3 ± 0.1	6.2± 0.2
Sub-adult male	125.2 ± 4.2	19.5 ± 1.1	13.8 ± 0.5	41.5 ± 1.2	2.3 ± 0.1	6.3 ± 0.2
Adult Male	174.6 ± 6.2	22.5 ± 1.0	16.5 ± 0.2	47.3 ± 1.1	3.3 ± 0.1	7.4 ± 0.2
Adult Female	86.7 ± 2.1	22.3 ± 1.0	21.0 ± 0.5	51.5 ± 1.1	2.5 ± 0.1	4.9 ± 0.1

a Linear regression equation, Min cADL = 2.22 * age (months or years) - 2.5533, R2 = 0.7006, P = 0.050
b Linear regression equation, Max cADL = 0.2357 * age (months or years) + 1.3571, R2 = 0.7479, P < 0.000

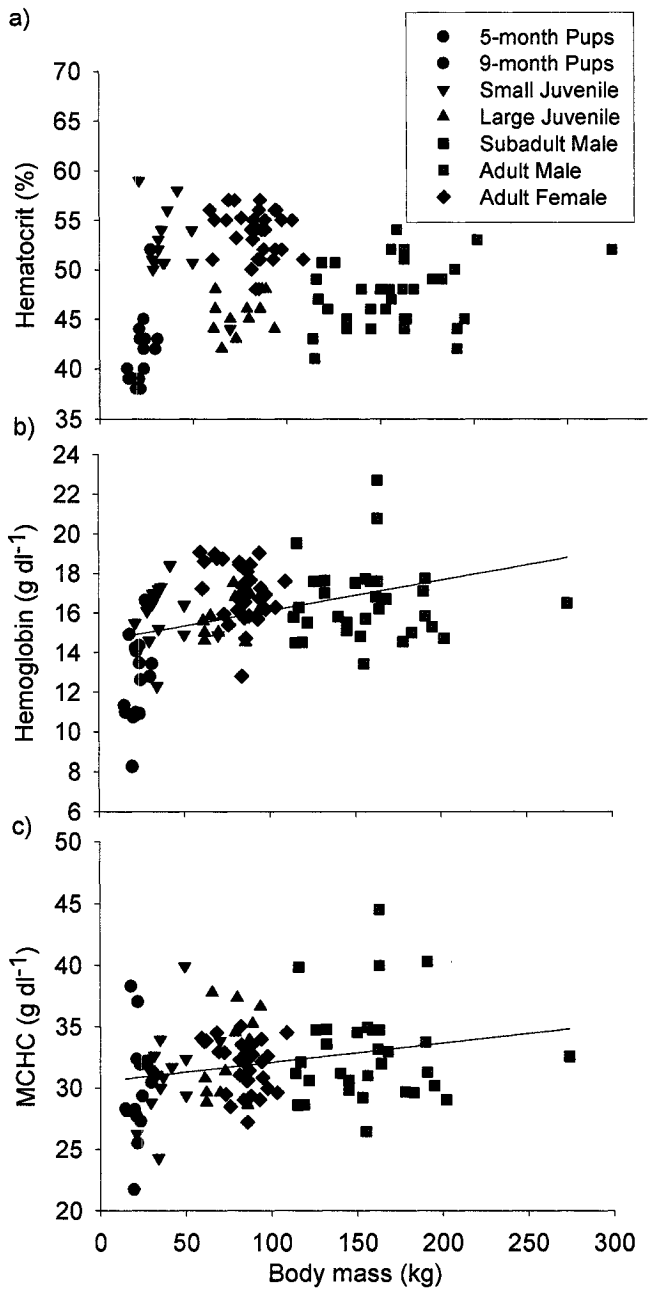

Figure 1. Developmental changes in a) hematocrit, b) hemoglobin content, and c) mean corpuscular hemoglobin content as a function of body size in California sea lions from 5-month old pups to adults (5-month pups, n=13; 9-month pups, n=7; small juvenile, n=18; large juvenile, n=12; sub-adult male, n=15; adult male, n=22; 87 kg adult female, n=37). For all animals combined the relationship between body size and Hct was not significant (r^2=0.01, P=0.413), whereas there was a significant linear relationship with Hb (r^2=0.14, P<0.001) and MCHC (r^2=0.06, P=0.009).

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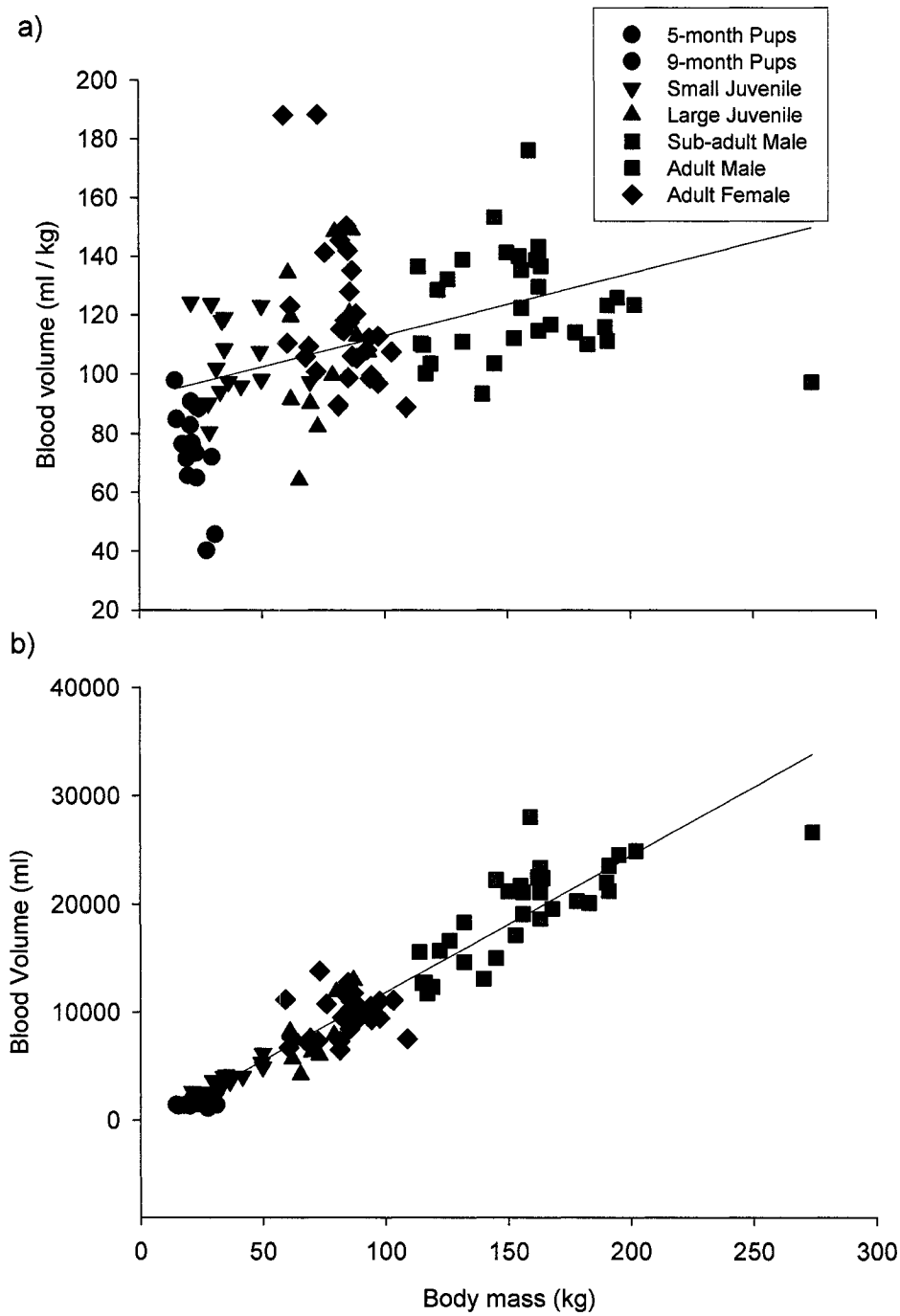

Figure 2. Developmental change in a) mass-specific blood volume and b) absolute blood volume with increasing body size in California sea lions from 5-month old pups to adults. There was a significant linear relationship during the development of absolute (r^2=0.92, P<0.001) and mass-specific blood volume (r^2=0.20, P<0. 001).

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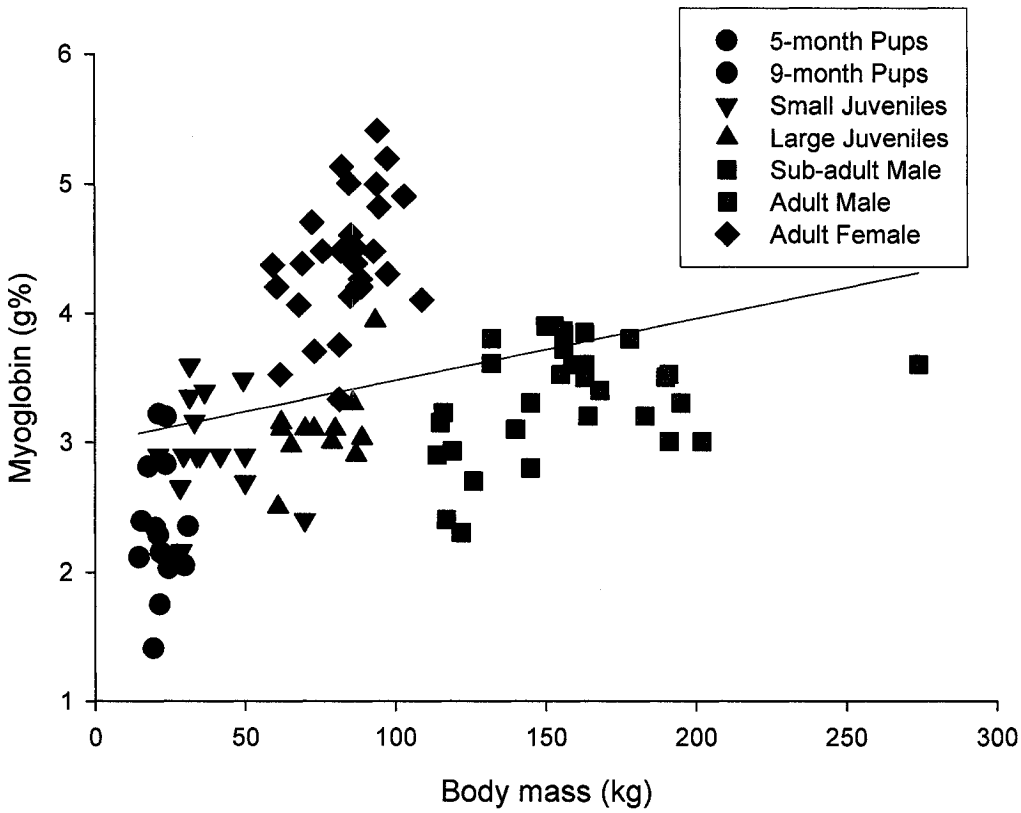

Figure 3. a) Mean muscle myoglobin content in relation to body size for California sea lions from 5-month old pups to adults. Line represents least-squares regression (r^2=0.10, P=0. 001).

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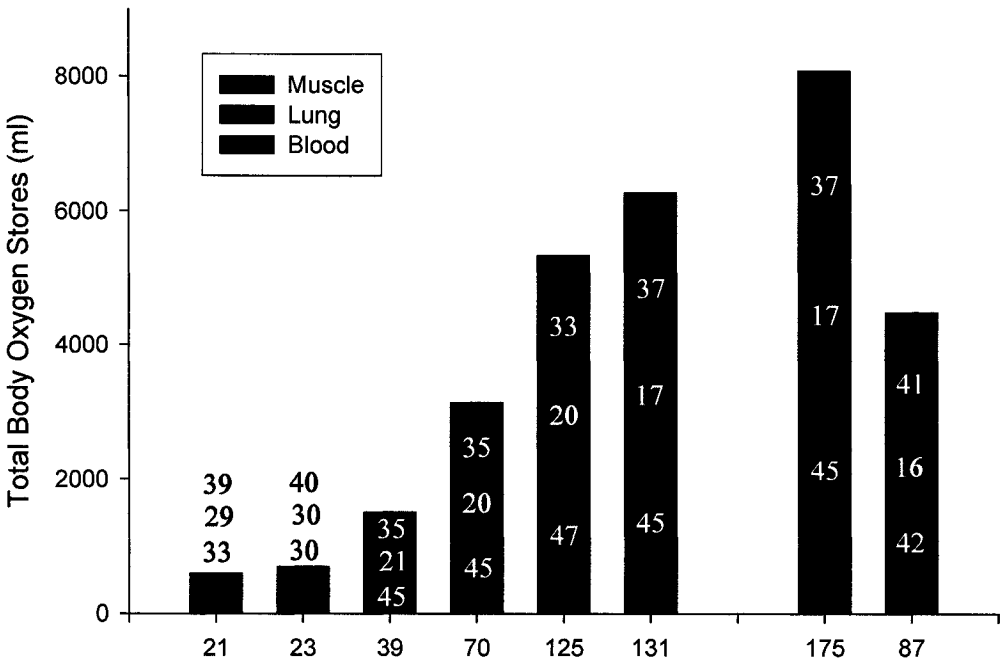

Figure 4. Comparison of absolute total body oxygen stores in the blood, lung, and muscle of California sea lions during their development from 5-month old pups to adults. Percentage of oxygen stores in blood, muscle, and lung are listed in text for each compartment.

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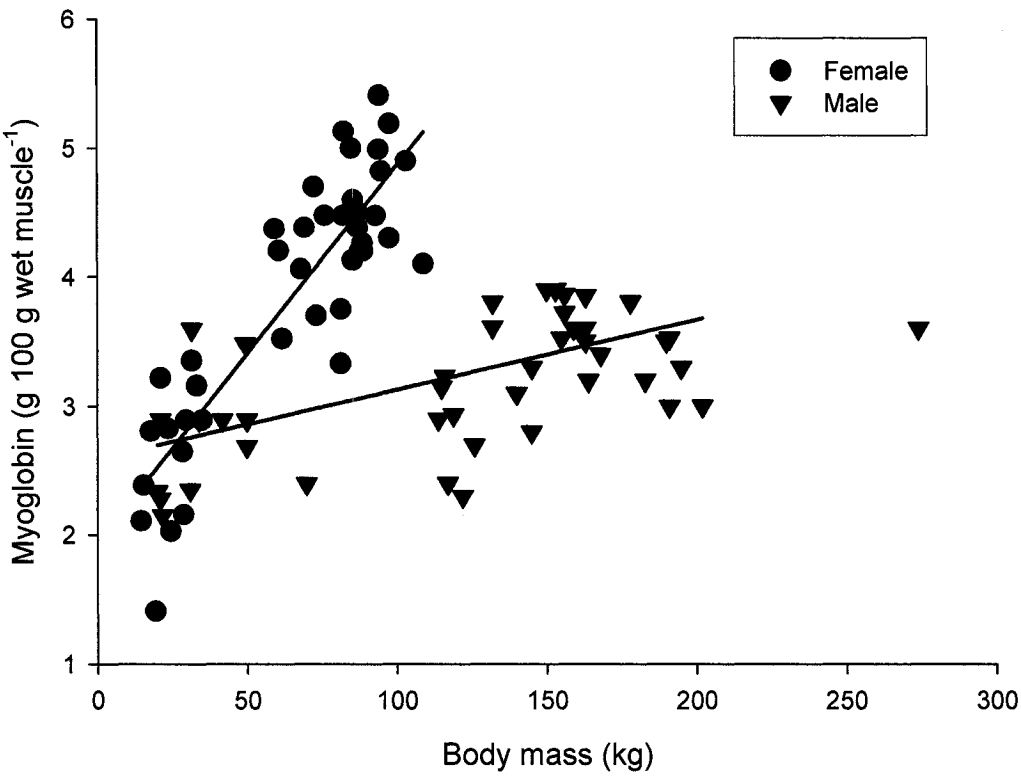

Figure 5. Muscle myoglobin as a function of body size for male and female California sea lions from pup size through adulthood. The relationship between body size and myoglobin was significant for males ($y=0.005x+2.56$; $r^2=0.36$, $P<0.001$) and females ($y=0.03x+1.95$; $r^2=0.78$, $P<0.001$), and the rate of development was significantly different for the sexes.

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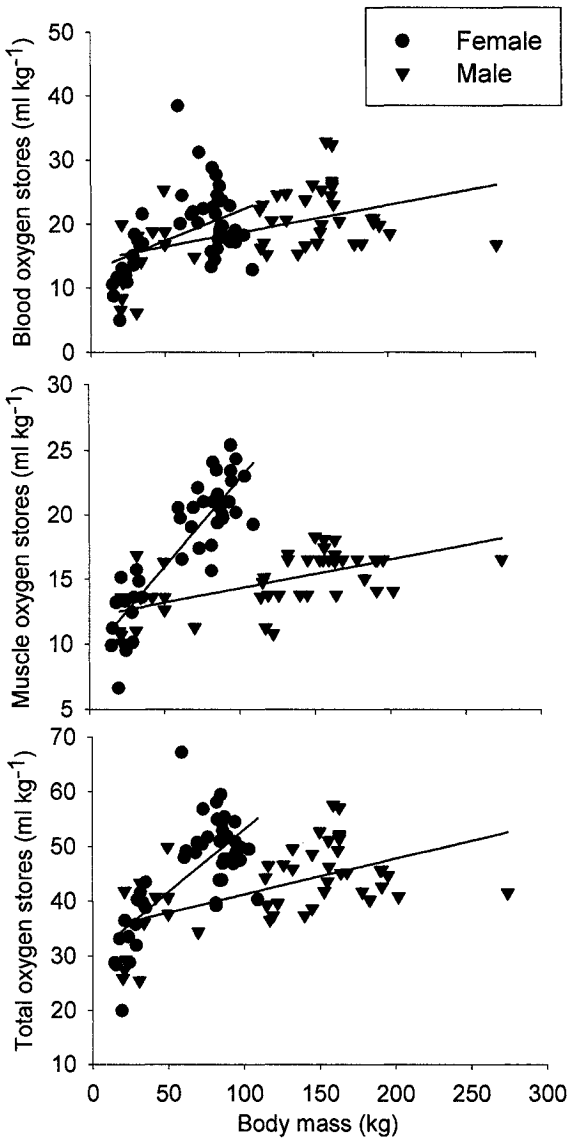

Figure 6. Mass-specific a) blood oxygen stores, b) muscle oxygen stores, and c) total oxygen stores as a function of body size was significant for male and female California sea lions. The relationship between body size and mass-specific blood oxygen stores was significant for females ($y=0.094x+12.66$; $r^2=0.20$, $P=0.002$) and males ($y=0.03x+14.29$; $r^2=0.99$, $P=0.001$), and significant for muscle oxygen stores in females ($y=0.14x+9.13$; $r^2=0.78$, $P<0.001$) and males ($y=0.02x+12.06$; $r^2=0.37$, $P<0.001$), and total oxygen stores for females ($y=0.23x+30.04$; $r^2=0.50$, $P<0.001$) and males ($y=0.07x+35.60$; $r^2=0.30$, $P<0.001$). However, the rate of development in mass-specific muscle oxygen stores was greater in females than males while the no greater in blood and total oxygen stores.

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