The effects of El Niño on the foraging behavior of lactating California sea lions (*Zalophus californianus californianus*) during the nonbreeding season

S.R. Melin, R.L. DeLong, and D.B. Siniff

Abstract: We compared the nonbreeding-season foraging behavior of lactating California sea lions (*Zalophus californianus californianus* (Lesson, 1828)) at San Miguel Island, California, during El Niño conditions in 1993 and non-El Niño conditions in 1996. Lactating females were instrumented with satellite-linked time–depth recorders between January and March in 1993 (n = 6) and 1996 (n = 10) and data were collected through May in each year. Females foraged northwest of the colony, up to 367 km from it and 230 km from the California coast. Mean dive depths ranged from 19.5 to 279.3 m, but most females achieved dives deeper than 400 m. Most females fed exclusively in the offshore habitat, traveled farther from the colony, spent more time traveling, made deeper and longer dives, and terminated lactation earlier during the 1993 El Niño. The results suggest that prey were concentrated in the offshore habitat and located farther from the colony and deeper in the water column during El Niño. Females did not change their foraging direction, foraging-trip duration, foraging effort, or prey species consumed.

Résumé : Nous comparons le comportement de recherche de nourriture hors de la saison de reproduction chez des lions de mer de Californie (*Zalopus californianus californianus* (Lesson, 1828)) pendant l'allaitement à l'île San Miguel, Californie, durant un épisode d'El Niño en 1993 et une période sans El Niño en 1996. Des femelles nourricières ont été munies de chronobathymètres enregistreurs reliés aux satellites entre janvier et mars en 1993 (n = 6) et en 1996 (n = 10) et les données recueillies jusqu'à la fin de mai à chacune des années. Les femelles recherchent leur nourriture vers le nord-ouest, jusqu'à 367 km de la colonie et 230 km de la côte californienne. Les profondeurs moyennes des plongées individuelles varient de 19,5 à 279,3 m, mais la plupart des femelles font des plongées de plus de 400 m. Durant l'épisode d'El Niño de 1993, la plupart des femelles se nourrissaient exclusivement dans l'habitat du large, se déplaçaient plus loin de la colonie, passaient plus de temps à leurs déplacements, faisaient des plongées plus profondes et plus prolongées et mettaient fin à l'allaitement plus tôt. Nos résultats laissent croire que les proies étaient concentrées dans les habitats du large et situées plus loin de la colonie et plus profondément dans la colonne d'eau durant l'épisode d'El Niño. Les femelles n'ont cependant pas modifié la direction dans laquelle elles recherchaient leur nourriture, ni la durée de leurs déplacements de recherche de nourriture, ni leur effort de recherche, ni les espèces de proies consommées.

[Traduit par la Rédaction]

Introduction

The California Current is a boundary current along the west coast of North America, extending from Canada to Mexico. The California Current is productive year-round but maximum productivity occurs between March and May, when strong offshore winds create upwelling along the coast (Lynn and Simpson 1987). This ecosystem provides habitat for many marine species, both seasonal migrants and permanent residents. Since 1976 the California Current has experienced low primary and secondary productivity and several El Niño events that have significantly changed the productivity of the system at all trophic levels (Hayward et al. 1999). The abundance of many marine species has declined significantly during this period, but California sea lions (*Zalophus californianus californianus* (Lesson, 1828)), a top predator and permanent resident in the California Current, have increased in numbers, reflecting an average population growth rate of 5.6% annually (Carretta et al. 2005).

The geographic distribution, foraging ecology, breeding, parental care, and social system of California sea lions have evolved under the influence of the seasonal upwelling and periodic El Niño events in the California Current. Sea lions breed on the California Channel Islands and offshore islands of Baja California, Mexico (Peterson and Bartholomew 1967; Aurioles et al. 1983; Antonelis et al. 1990; Melin and DeLong 2000). Adult males disperse from the breeding colonies during the nonbreeding season and migrate northward as far as southeast Alaska (Odell 1981; Maniscalco et al.

Received 26 July 2007. Accepted 12 November 2007. Published on the NRC Research Press Web site at cjz.nrc.ca on 29 February 2008.

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 doi:10.1139/Z07-132 © 2008 NRC Canada

2004). Juveniles and nonlactating females frequent the colonies or disperse along the California coast (Odell 1981). Lactating females, however, are nonmigratory and return to the breeding colony regularly throughout the year to nurse their pups (Odell 1981; Melin et al. 2000).

Because they are nonmigratory, lactating females are vulnerable to the seasonal, annual, and multiyear fluctuations in the productivity of the system. The breeding season extends from May to July, during which time females give birth to a single pup. Between 5 and 7 days after giving birth, females begin an attendance cycle, alternating foraging trips to sea with nursing visits on land until the pup is weaned at 8–11 months (Odell 1981; Melin et al. 2000). During the 3-month breeding season, the pup remains ashore fasting while the female feeds at sea for 2 or 3 days at a time. Thus, females are restricted in the time they may be away from the colony because the pup is solely dependent on them for sustenance. The nonbreeding season extends from August through April. During this time the pup becomes more independent, and by 6 months of age, most pups are supplementing their milk diet with solid food. Females now leave the pups for longer periods of time, up to 5 days (Melin et al. 2000), but the energetic demands of lactation may increase as the pup grows (Oftedal et al. 1987) and pregnant females must allocate some energy resources to maintaining a pregnancy in addition to lactation. Furthermore, seasonal shifts in the distribution, abundance, or availability of prey occur during the 9 months of the nonbreeding season (Bailey et al. 1982; Jefferts 1983; MacCall and Stauffer 1983; Larson et al. 1994; Sakuma and Ralston 1997; Schwartzlose et al. 1999) and lactating females must continually relocate prey fields. Consequently, lactating females show greater variability in foraging behavior during the nonbreeding season than during the breeding season as they expand their foraging area and adjust their behavior in response to prey movements (Melin and DeLong 2000).

Lactating California sea lions are sensitive to prolonged changes in their foraging environment. El Niño events in 1982–1983 and 1992–1993 reduced the availability and abundance of sea lion prey for 13 months (Arntz et al. 1991) and 25 months (Hayward et al. 1994), respectively. The California sea lion population responded with a total decline in pup production of 35% in 1983 and 27% in 1992 for all colonies (Carretta et al. 2005). During the 1982–1983 El Niño, lactating California sea lions at San Miguel Island spent more time diving and swimming, had longer dive bouts and dive durations (Feldkamp et al. 1991), expended more energy per foraging trip (Costa et al. 1991), and changed their diet (DeLong et al. 1991) during the breeding season in response to the poor foraging conditions. However, the changes in behavior were not sufficient to support the energetic cost of reproduction; pup production declined 30% at this colony and the high pup mortality rate (13.7%, doubled from previous years) indicated that females could not support lactation (DeLong et al. 1991). Pup production at all the colonies began increasing in 1984 but remained low after the 1982–1983 El Niño, recovering to pre-El Niño levels 5 years later, in 1988, indicating that significant juvenile and adult mortality also occurred during this event (DeLong et al. 1991; Carretta et al. 2005). In contrast, after the 1992–1993 El Niño, pup production at all the colonies remained depressed in 1993, increased significantly in 1994, and rebounded 52% by 1995 (Carretta et al. 2005). The breeding-season foraging behavior of lactating females was not studied during the 1992–1993 El Niño, but the low reproduction rate suggests that females had difficulty finding enough food to support reproduction in 1992 and 1993. The quick recovery of production by 1995, however, indicated that adult mortality was not significant during the 1992–1993 El Niño and that females were able to meet their own energetic needs.

The effect of El Niño conditions on the foraging behavior of lactating California sea lions during the nonbreeding season has not been investigated. Yet the nonbreeding season represents 66% of the time a female invests in her pup and all of the time invested in her pregnancy. Thus, the behavioral response to El Niño conditions during the nonbreeding season may affect a female's reproductive success by affecting the survival of her current offspring and the success of her pregnancy. Between November 1991 and December 1993, El Niño conditions characterized by elevated sea-surface height, widespread positive anomalous sea-surface temperatures, low primary and secondary productivity, and a deeper nutricline were present along the California coast (Hayward 1993; Hayward et al. 1994). In 1996, oceanographic conditions were very productive, as mild La Niña conditions dominated the California Current, with normal or higher than normal upwelling and productivity along the California coast (Schwing et al. 1997). In 1996, landings of Pacific sardine (*Sardinops sagax* (Jenyns, 1842)), northern anchovy (*Engraulis mordax* Girard, 1854), Pacific mackerel (*Scomber japonicus* Houttuyn, 1782), jack mackerel (*Trachurus symmetricus* (Ayres, 1855)), and California market squid (*Loligo opalescens* Berry, 1911), the primary prey of California sea lions, were double those in 1993, suggesting that prey were more abundant in 1996 (California Department of Fish and Game 1997). The aim of this paper is to compare the nonbreeding-season behavior of lactating females during El Niño conditions in 1993 and non-El Niño conditions in 1996. We expected significant differences in foraging behavior of lactating females in the 2 years as they strove to meet the energetic demands of late lactation under different foraging conditions.

Materials and methods

Study site and design

Lactating California sea lions were captured at the Point Bennett colony on San Miguel Island, California (34.03°N, 120.44°W). Females were instrumented with satellite-linked time–depth recorders (SLTDRs) and VHF transmitters in January 1993 (n = 6) and January or March 1996 (n = 10). Data were collected between January and May in each year. The SLTDRs transmitted for 8 h each day. Location, dive-depth, and dive-duration data were stored, summarized, and transmitted to National Oceanic and Atmospheric Administration (NOAA) satellites at 6 h intervals each day. VHF radio transmitter signals at 1 pulse per second were used to determine foraging-trip duration. A remote receiver system (Advanced Telemetry Systems, Isanti, Minnesota) consisting of a programmable receiver, data logger, and battery was located near the colony. The system was programmed to con-

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Table 1. Percentages and quality of satellite telemetry positions for California sea lions (*Zalophus californianus californianus*) obtained from NOAA satellites, processed by System Argos, and used in the analyses.

	Percentage of locations						
	1993 El Niño		1996 non-El Niño conditions		Position error (km)		
Location quality	Land (n = 159)	Sea (n = 281)	Land (n = 291)	Sea (n = 268)	n	Mean ± SE	Range
3	7.9	0.0	15.2	0.8	7	0.7±0.1	0.3–1.2
2	10.5	0.4	27.3	2.2	12	0.8±0.2	0.1–2.1
1	47.4	25.3	15.1	10.4	15	1.7±0.4	0.4–6.1
0	3.9	10.3	21.2	19.4	12	4.5±0.6	1.5–8.8
A	13.2	51.9	15.1	28.0	13	2.5±0.4	0.8–6.7
B	17.1	12.1	6.1	39.2	65	5.9±2.8	1.5–20.0

Note: Locations range in quality from B (poorest) to 3 (best). The land positions were for San Miguel Island, California. The mean ± 1 SE, minimum, and maximum error associated with on-land satellite telemetry locations were obtained from instruments placed at a known location at San Miguel Island.

tinuously scan each transmitter frequency for 10 s every 20 min. The data were downloaded every 2 months and the days and hours that each animal was present were summarized using a computer program. Females were considered present if 3–10 transmissions were received during each scan for 3 consecutive hours or longer. The female was absent if no transmissions were received for periods longer than 3 h. If fewer than 3 or more than 10 transmissions were received during each scan over a 3 h period, the transmissions were considered to be intermittent or to represent interference and the female did not change status. Foraging-trip duration was calculated as the time elapsed between the last reliable signal received before departure and the first reliable signal received upon return to the colony. VHF radio transmitter data were obtained for all females that returned to the colony. California sea lions do not travel far from the colony with their dependent pups (Melin et al. 2000), and remote receiver systems were located near the two areas where females and pups aggregate; thus, if females were not detected at the colony for a month or more during the study, we assumed that they had terminated lactation and that data collected after they departed represented postlactation behavior.

El Niño conditions existed throughout the range of California sea lions during the nonbreeding season in 1993 (Hayward et al. 1994); in 1996, strong upwelling and high productivity associated with mild La Niña conditions dominated the California Current (Schwing et al. 1997). We used individual females as the sampling unit and compared the behavior of lactating females in 1993 and 1996 in order to describe behavior under different marine conditions. We divided the study period into winter (15 January – 15 March) and spring (16 March – 20 May) to investigate seasonal changes in behavior of lactating females. Paired t tests were used to compare the foraging distribution and diving-behavior parameters for lactating females between seasons within each year. We found no seasonal differences in distribution or diving behavior in either year, so the data within each year were pooled for analyses.

Foraging distribution

Location processing

Location data obtained from satellites were summarized by Service Argos (Service Argos, Inc.1996). To estimate the error associated with satellite locations, each SLTDR was placed at a known position at San Miguel Island (UTM, 34.03°N, 120.44°W) and left to transmit for 24 h. The mean error of locations relative to the known position ranged from 0.7 to 5.9 km and the maximum error was 20.0 km (Table 1). Each location was inspected to determine whether it should be retained for the analysis. A Microsoft Excel® macro was used to automatically filter the locations on a point-to-point basis using a maximum swim speed of 3 $m \cdot s^{-1}$ (Feldkamp et al. 1989; Ponganis et al. 1990) and the elapsed time between consecutive locations to determine whether the location was within the swimming capabilities of the animal. Locations were discarded if the distance between the two points was greater than the possible travel distance of the animal during the elapsed time.

To minimize dependence among locations obtained on each foraging trip, only one location was selected for each day for each female. When more than one location was obtained for the same day, the location with the best System Argos-rated quality was used in the analysis (Melin 2002). If multiple locations on the same day had the same quality, a single location was randomly chosen among all the locations with the same quality. After the analyses of individual diving behavior were completed from time–depth recorders, it was determined that the average minimum travel time was 3 h (n = 9, SE = 1.1 h) between departure from the colony to the first foraging bout in both years. Therefore, only locations more than 30 km from the colony (travel speed 10.8 $km \cdot h^{-1}$) were included in the analyses of foraging distance and direction to avoid using locations obtained while the female was traveling from the colony to foraging areas.

Distance and direction of foraging

The distance and direction of each foraging location relative to the colony were determined by using a fixed latitude and longitude at San Miguel Island (34.03°N, 120.44°W) as the point of origin and measuring the straight-line distance and bearing to each location. The median of all the distances and bearings for each trip was used as the measure of distance and direction for each trip for each female. A trip mean was calculated from the medians. A vector summarizing the distance and direction of all trips was created for each female by converting the mean distances and bearings into Cartesian coordinates (Zar 1996). The mean bearing for each female was classified into northeast (0°–90°), southeast (91°–180°), southwest (181°–270°), or northwest (271°–360°) for qualitative descriptions of foraging direction from the colony.

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Ocean habitats and zones

We classified the foraging locations and dive-depth data for each female into ocean habitats and zones as an index of habitat preference. Depth contours from 100 to 1000 m were associated with each location using a spatial join function in ArcView® version 3.2 that matched each location with the nearest bathymetric value. The hydrographic data were used to classify ocean habitats as follows: shelf ≤200 m, slope >200 and <1000 m, and offshore ≥1000 m (Lynn and Simpson 1987). Each female was assigned an ocean habitat based on the habitat with the highest percentage of her locations over the study period.

Ocean zones that described the vertical dimension in which dives were made were classified as epipelagic (0–200 m), mesopelagic (>200 and <1000 m), and bathypelagic (≥1000 m). The ocean zone for each female was determined from the SLTDR histogram data and allowed classification for most females. Each female was assigned an ocean zone based on the zone with the greatest percentage of her dives over the study period.

Activity patterns, diving behavior, and diving effort

Dive data were obtained using two methods. The SLTDR collected dive data in histogram form and transmitted them to a satellite. The data provided general descriptions of diving behavior and were available for all SLTDRs regardless of whether the instrument was recovered at the end of the deployment. Each SLTDR was equipped with a microprocessor-controlled TDR. TDRs recorded individual dive depths and dive durations in real time and stored the data in the SLTDR. The TDR data provided a detailed description of activity patterns, diving behavior, and diving effort, but were only available if the instrument was recovered at the end of deployment. Complete sets of the TDR data were used in the analyses of activity patterns and diving effort, but diving behavior data (dive depth and dive duration) were subsampled to reduce dependence due to bout-diving. A random sample of 25% of all the dives for each female was used in the analyses to calculate mean dive depth and duration.

SLTDR data

SLTDR dive-depth and -duration data were stored in histogram bins that were determined prior to deployment. Dive depths were measured in 4 m increments; the minimum depth considered to be a dive was 8 m. The first dive-depth bin was 8–75 m and the upper limits for the remaining bins were 150, 225, 300, 375, and >375 m. The upper limits of the dive-duration bins were defined as 1, 2, 4, 6, 8, and >8 min. SLTDR dive data were analyzed by summing the counts of dives in each depth and duration bin for each trip for each female. The percentage of dives in each bin was calculated for each trip and the trip percentages were arcsine-transformed (Zar 1996) to calculate mean percentages for each female during the deployment period. The means for the females in each year were used to calculate an annual mean for each depth and duration bin.

To investigate daily patterns of diving behavior, each day was divided into four periods based upon the average time of sunrise and sunset at San Miguel Island during the study period: daytime (0900–1459), dusk (1500–2059), nighttime (2100–0259), and dawn (0300–0859). The classification of dive pattern was based on a combination of behavior relative to time of day and dive depth. "Diel" refers to a distinct change in diving behavior with time of day. Dive-depth patterns were classified as shallow (60% of dives ≤75 m), deep (60% of dives >75 m), or mixed.

TDR data

Activity patterns

Activity patterns were described only for females for which TDR data were recovered. In 1993, the TDRs were duty-cycled; only complete trips were used in the analyses of activity patterns and diving behavior. For each trip the percentages of time spent traveling, bout-diving, and swimming and resting (interbout time) were calculated. Time spent traveling was the sum of transit time outbound from the colony to the location of the first foraging bout and transit time inbound to the colony after the last foraging bout. The time spent bout-diving was the sum of the time spent diving in bouts and the time spent at the surface within a dive bout. The TDRs did not reliably record resting time while the animals were at sea, so the time spent resting could not be parsed from the time spent swimming. Consequently, the interbout time was the sum of nonbout dive durations, nonbout surface intervals, and swimming and resting time.

Diving behavior

Mean dive depths and dive durations were calculated on the basis of bout dives only. Bout dives were divided into the same daily periods as the SLTDR dive data for a comparison of daytime (0900–1459) and nighttime (2100–0259) dive depths for individual females. This analysis yielded mean dive depth during the day and night and complemented the dive-pattern analysis from the SLTDR data.

Diving effort

Diving effort on each foraging trip was assessed using the number of dive bouts, duration of dive bouts, number of dives per hour in each bout, and the duration of interbout surface intervals. The onset of a dive bout was defined as a series of at least five dives to a depth greater than 8 m and for which the surface time between dives did not exceed the bout-ending criterion (Feldkamp et al. 1989). The bout-ending criterion was unique to each individual female and was determined by a log-survivorship curve (Feldkamp et al. 1989; Harcourt et al. 1995) of the surface intervals between dives. A Microsoft Excel® macro was used to automatically determine the beginning and end of each bout, based on the bout-ending criterion for each female. The duration of a bout was the sum of the dive durations and the surface time between dives in the bout. The interbout surface interval was the sum of dive durations and surface time between bouts and indicated the amount of time elapsed between concentrated diving periods.

Food habits

Scats (fecal samples) were collected in late March 1993 and early May 1996 from haul-out areas used by adult female California sea lions at San Miguel Island. The processing of samples followed Orr and Harvey (2001). Percent occurrence of a prey species was calculated from the count

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of scats with that species present divided by the total number of scats containing identifiable prey parts, including fish otoliths, fish bones, and cephalopod beaks.

Statistical analyses

We tested the hypothesis that foraging behavior during El Niño conditions in 1993 did not differ from that during non-El Niño conditions in 1996. We used a nested ANOVA in which each foraging trip for each female was used as a repeated sample and each female was a sampling unit nested within a year (Winer 1971). The p values reported are for ANOVA tests unless otherwise noted. The Bonferroni adjustment was used to adjust p values for multiple-comparison tests unless otherwise noted. Systat® 10.0 and Microsoft Excel® 2000 were used for all statistical comparisons. Statistical significance was $\alpha = 0.05$.

Comparisons of percent occurrence between scat samples collected during El Niño and non-El Niño conditions were conducted using χ^2 analyses. Because of the rapid digestion that occurs in pinniped stomachs, percent occurrence is considered an index of the occurrence of a prey species in the diet. Percent occurrence may be biased toward prey species that have otoliths and bones that are robust and therefore more resistant to the digestive process, and that are consumed during the last 24–48 h of the foraging trip (Orr and Harvey 2001).

Results

In total, 281 and 268 at-sea locations were retained for analyses for 6 females in 1993 and 10 females in 1996, respectively (Tables 1, 2). Deployments lasted between 40 and 128 days and included between 2 and 18 foraging trips for each female (Table 2). Most of the location qualities while the animals were on land were class 0 or above (69.7% in 1993, 78.8% in 1996), while most of the locations obtained while the animals were at sea were class 0 or below (73.3% in 1993, 86.6% in 1996). SLTDR dive data were obtained for 15 of 16 females and TDR dive data were obtained for 9 females (Table 2).

Foraging distribution

Lactating females foraged mostly northwest of San Miguel Island (83.3% in 1993, 80.0% in 1996) (Table 3, Fig. 1). One female in 1993 and two females in 1996 fed northeast of the island (Table 3, Fig. 2). Females rarely traveled south of San Miguel Island. In 1993, most females used the offshore habitat (83.3%), but in 1996, females occupied all habitats and only two of eight females (25%) fed exclusively offshore (Table 3, Fig. 2). Females utilizing the northeast foraging area were located primarily over the shelf or slope. Individual females tended to use only one ocean habitat but four females (25%) used multiple habitats (Table 3). Of the females that used multiple habitats, one female (96492) shifted from the northeast shelf habitat in the winter to the slope in the spring, and one female (96553) shifted from the northwest offshore habitat in the winter to the shelf and slope in the spring. The latter female showed a seasonal shift to deeper diving while in the offshore habitat (≥75 m) to shallow diving in the slope habitat (<75 m). Females primarily used the epipelagic zone in both years (87.5%). Two females, feeding offshore in 1993, used the mesopelagic zone. The data were too sparse to conduct statistical tests to examine relationships among dive pattern, ocean zone, and ocean habitat. However, we simplified the dive pattern into shallow and nonshallow (mixed and deep) for dive depth, and diel and nondiel for daily diving pattern, to describe relationships between ocean habitat and dive pattern. We found no association between ocean habitat and dive depth ($\chi^2 = 1.02$, $\chi^2_{0.05;[1]} = 3.841$, $p > 0.25$) or ocean habitat and daily dive pattern ($\chi^2 = 0.097$, $\chi^2_{0.05;[1]} = 3.841$, $p > 0.75$).

For individual females, the mean distance traveled from the colony ranged from 46.7 to 281.8 km; the maximum distance was 366.6 km (Table 3). The mean distance from the California coast ranged between 1.9 and 98.8 km for individual females and the maximum distance was 229.5 km (Table 3). The mean foraging distance from the colony was 161.0 and 101.2 km in 1993 and 1996, respectively (Table 4). The mean foraging distance from the mainland coast was 60.7 and 44.1 km in 1993 and 1996, respectively. Lactating females foraged farther from the colony ($F_{[1,14]} = 14.459$, $p < 0.001$) and farther from the California coast during the 1993 El Niño ($F_{[1,14]} = 19.944$, $p < 0.001$) than during the 1996 non-El Niño conditions (Table 4). Within each year, individual females showed significant variability in all the foraging-distribution parameters (Table 4).

Activity patterns, diving behavior, and diving effort

SLTDR dive data

SLTDR dive histograms were obtained for six females in 1993 and nine females in 1996 (Table 2). In 1993, 38.3% of the dives were to between 8 and 75 m and 41.8% were to between 75 and 300 m (Fig. 3). In 1996, 74.2% of the dives were to between 8 and 75 m and 24.0% were to between 75 and 300 m. In 1993, 21.2% of the dive durations were up to 1 min and 48.7% of the dives were between 3 and 6 min long (Fig. 4). In 1996, 41.6% of the dives lasted up to 1 min and 31.7% of the dives were between 3 and 6 min long. Overall, dives were deeper and longer during El Niño conditions in 1993 than during non-El Niño conditions in 1996 (dive depth, $\chi^2 = 6075.0$, $\chi^2_{0.05;[5]} = 11.070$, $p < 0.001$; dive duration, $\chi^2 = 4718.2$, $\chi^2_{0.05;[5]} = 11.070$, $p < 0.001$).

TDR dive data

Activity patterns

The activity patterns during foraging trips were summarized from the TDR records of three females in 1993 and six females in 1996 (Table 2). The feeding-trip durations and activity patterns of females were similar in the 2 years (Table 4). Females spent 44.6% and 50.2% of their time bout-diving, 37.3% and 39.3% of their time swimming or resting between diving bouts (interbout time), and 18.1% and 10.5% of their time traveling in 1993 and 1996, respectively (Table 4). There were no differences in foraging-trip duration, bout-diving, interbout time, or hours spent in transit outbound between the 2 years. However, the total percentage of time females spent traveling per trip was greater for females during the1993 El Niño ($F_{[1,7]} = 8.680$, $p = 0.005$) because more time was spent in transit inbound to the colony in 1993 ($F_{[1,7]} = 6.091$, $p = 0.017$), and the

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Table 2. Sample sizes, number of days deployed, and data used in analyses of the foraging behavior of California sea lions (*Zalopus californianus californianus*) at San Miguel Island, California, between January and May in 1993 and 1996.

					Lactation		Post lactation			
	ID No.	Season	No. of days	Departure from colony	No. of trips	No. of at-sea locations	No. of trips	No. of at-sea locations	PTT dive data?	TDR dive data?
1993 El Niño	93044	W, S	113	12 April	8	62	6	28	Yes	Yes
	93184	W, S	96	20 March	2	10	8	55	Yes	No
	93245	W, S	99	9 March	4	22	2	27	Yes	No
	93302	W, S	118	None	18	30			Yes	Yes
	93305	W, S	103	21 April	7	21	5	30	Yes	Yes
	93325	W, S	83	22 April	11	19			Yes	No
Mean ± SE			102±5.1	4 April ± 9 days	8.3±2.3	27.3±7.4	5.3±1.3	35.0±6.7		
1996 non-El Niño conditions	96202	W, S	128	27 May	14	34	—	—	Yes	Yes
	96213	W, S	93	7 May	12	21	—	—	Yes	No
	96433	S	56	22 April	5	21	—	—	Yes	No
	96492	W, S	127	17 May	18	39	—	—	Yes	No
	96532	S	48	None	6	34	—	—	Yes	Yes
	96553	W, S	121	27 May	13	55	—	—	Yes	Yes
	96574	W, S	43	None	4	14	—	—	Yes	No
	96633	S	50	None	5	20	—	—	No	Yes
	96673	S	52	15 May	6	19	—	—	Yes	Yes
	96714	W	40	21 April	4	11	—	—	Yes	Yes
Mean ± SE			75.8±11.6	10 May ± 5.7 days	8.7±1.6	26.8±4.3	—	—		

Note: "Departure from colony" indicates the date when females permanently departed from the colony (i.e., termination of lactation); "none" indicates that a departure was not detected (W, winter; S, spring).

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Table 3. Foraging-distribution parameters for individual lactating California sea lions (*Zalopus californianus californianus*) at San Miguel Island, California, between January and May in 1993 and 1996.

			Distance from colony (km)		Distance from coast (km)						
ID No.	No. of trips	No. of locations	Mean ± SE	Max.	Mean ± SE	Max.	Direction	Ocean habitat	Ocean zone	Dive depth	Diel diving?
1993 El Niño											
93044	8	34	187.0±22.6	320.7	64.3±9.5	169.4	NW	Offshore	E	Mixed	Yes
93184	2	10	136.2±41.5	248.5	65.5±2.3	206.2	NW	Offshore	M	Mixed	Yes
93245	4	22	281.8±24.5	350.3	67.9±8.0	101.9	NW	Offshore	M	Deep	Yes
93302	18	30	46.7±3.3	107.8	13.8±1.7	30.2	NE	Slope	E	Deep	No
93305	7	21	233.4±40.7	366.6	98.1±11.8	222.9	NW	Offshore	E	Mixed	Yes
93325	11	19	81.1±9.3	185.3	54.5±9.8	168.0	NW	Offshore	E	Deep	No
1996 non- El Niño conditions											
96202	14	34	114.8±9.1	242.3	88.0±7.7	142.0	NW	Offshore	E	Shallow	No
96213	12	21	76.8±8.0	120.9	23.5±3.2	49.6	NW	Slope	E	Shallow	Yes
96433	5	21	79.1±19.0	143.2	44.0±14.2	97.9	NW	Slope	E	Mixed	Yes
96492	18	39	69.6±5.9	154.1	11.2±2.2	41.8	NE	Shelf or slope	E	Shallow	Yes
96532	6	34	120.4±7.7	225.0	51.8±5.9	110.0	NW	Slope	E	Shallow	Yes
96553	13	55	155.2±17.1	332.7	54.9±8.5	229.5	NW	Slope or offshore	E	Shallow	Yes
96574	4	14	70.8±18.3	138.5	13.0±2.0	28.3	NW	Shelf or slope	E	Mixed	Yes
96633	5	20	60.2±1.1	84.5	1.9±0.4	5.3	NE	Shelf	E	Shallow	Yes
96673	6	19	123.3±25.9	278.2	98.8±20.4	198.7	NW	Offshore	E	Shallow	No
96714	4	11	142.1±34.2	230.7	53.4±27.5	135.8	NW	Shelf or slope	E	Shallow	No

Note: Distances are the straight-line distance from colony or mainland coast (E, epipelagic; M, mesopelagic).

number of dives per hour on each foraging trip was lower during El Niño ($F_{[1,7]} = 27.944$, $p < 0.001$) (Table 4). Within years, there was considerable individual variability in all activity parameters except mean total percent time spent traveling and mean time in transit to the foraging area, which did not vary among females (percent time traveling, $p = 0.860$; travel time outbound, $p = 0.166$) (Table 4).

Diving behavior

The TDR data provided a detailed description of diving behavior and effort for nine females that also had SLTDR dive histogram data (Table 2). Like the SLTDR dive distribution, in 1996 most dives were shallow and short, but in 1993 diving was distributed over a greater range of depths. All females dove to depths greater than 250 m, and seven of nine females (78%) made dives that exceeded 400 m. The maximum dive depths exceeded the measuring capabilities of the instruments at 482 m. Dive depth was positively correlated with dive duration (Pearson's correlation, $r = 0.929$). The maximum dive duration was 16 min. Individual females had mean dive depths between 18.4 and 334.4 m (Table 5). In both years, females dove throughout the day and night but mean daytime dives were generally deeper than nighttime dives. Three of nine females (33.3%) showed diel diving, with significantly shallower dives at night than in the day.

In 1993, the mean dive depth was 194.2 m and the mean dive duration was 5.0 min (Table 4). In 1996, the mean dive depth was 70.2 m and the mean dive duration was 2.5 min. Females made deeper ($F_{[1,7]} = 104.691$, $p < 0.001$) and longer dives ($F_{[1,7]} = 66.269$, $p < 0.001$) in 1993 than in 1996. Mean daytime and nighttime dive depths were also greater during El Niño (daytime, $F_{[1,7]} = 27.095$, $p < 0.001$; nighttime, $F_{[1,7]} = 28.568$, $p < 0.001$).

Diving effort

The mean bout duration for individual females ranged from 1.8 to 7.9 h and the number of dives per hour in a bout ranged from 4.6 to 22.4 (Table 5). The maximum bout duration was 20.7 h. The mean interbout intervals were between 2.3 and 5.6 h, with a maximum of 38.0 h.

Females made fewer dive bouts per foraging trip and fewer dives per hour in each bout during El Niño (dive bouts, $F_{[1,7]} = 6.790$, $p = 0.012$; dives per hour in each bout, $F_{[1,7]} = 42.419$, $p < 0.001$) (Table 4). The mean dive-bout and interbout durations were not significantly different (Table 4).

Food habits

The most frequently occurring prey of female California sea lions during the spring in 1993 and 1996 were juvenile Pacific hake (*Merluccius productus* (Ayres, 1855)), Pacific sardine, California market squid, Pacific mackerel, rockfishes (*Sebastes* spp.), jack mackerel, and northern anchovy (Fig. 5). The primary species (>10% occurrence) consumed were the same in 1993 and 1996, with the exception of northern anchovy, which was only present in 1996. However, the occurrence of Pacific hake ($\chi^2 = 4.1$, $\chi^2_{0.05;[1]} = 3.841$, $p < 0.05$), Pacific sardine ($\chi^2 = 14.1$, $\chi^2_{0.05;[1]} = 3.841$, $p < 0.001$), and California market squid ($\chi^2 = 4.0$, $\chi^2_{0.05;[1]} = 3.841$, $p < 0.05$) increased between 1993 and 1996.

Postlactation foraging behavior

In 1993, five females (83.3%) dispersed from the colony in March and April and foraged from haul-out sites along the central California coast until returning to the colony in June (Table 2). One female frequented San Miguel Island throughout the study period. In contrast, in 1996, seven females (70.0%) made extended foraging trips exceeding 30 days in late April and May and three females continued to frequent San Miguel Island throughout the study period. Because California sea lions do not relocate away from the

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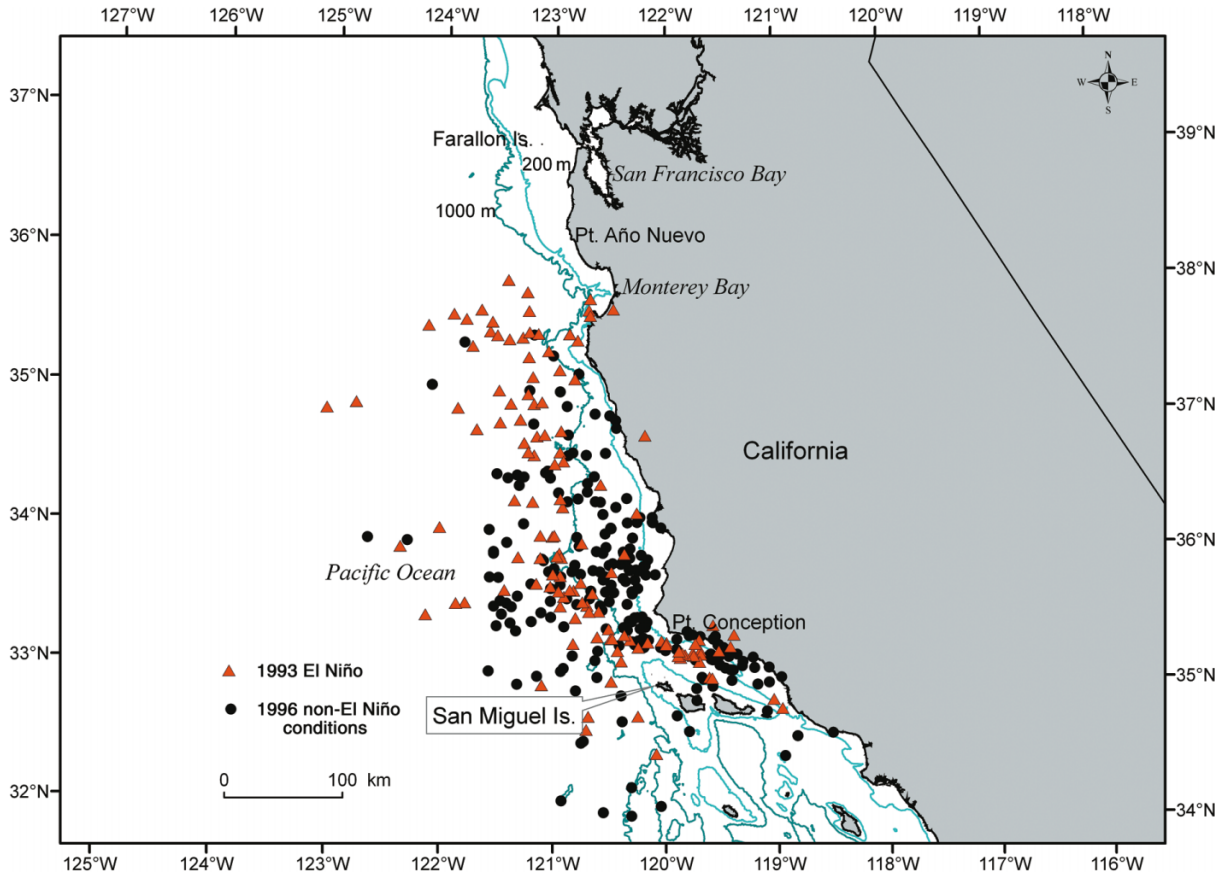
Fig. 1. At-sea distribution of lactating California sea lions (*Zalophus californianus californianus*) instrumented at San Miguel Island, California, in the nonbreeding seasons during the 1993 El Niño (6 females; n = 281) and 1996 non-El Niño (10 females; n = 268) oceanographic conditions.



colony with a dependent pup (Melin et al. 2000), we assumed that the extended periods spent away from the colony indicated the end of lactation (due either to weaning or pup mortality). Lactation ended earlier in 1993 (n = 5, mean = 4 April, SE = 9 days) than in 1996 (n = 7, mean = 10 May, SE = 5.7 days) (Table 1) (t test, p = 0.004).

Comparisons between the lactation and postlactation foraging behavior of females in the 2 years were not possible because in 1996, too few data were collected during the postlactation period. However, in 1993, four females departed San Miguel Island in the spring and we collected data for a month or longer after lactation terminated. The primary haul-out sites were northwest of San Miguel Island and included Point Buchon, Cape San Martin, Monterey Bay, and Año Nuevo Island along the central California coast. Females did not travel greater distances from their haul-out areas to feed during the postlactation period (lactation period, mean = 209.6 km, SE = 31.2 km; postlactation period, mean = 247.7 km, SE = 36.7 km; paired t test, p = 0.447). But females fed closer to the California coast during the postlactation period (lactation period, mean = 73.9 km, SE = 8.1 km; postlactation period, mean = 33.6 km, SE = 8.9 km; paired t test, p = 0.002). After feeding exclusively in the offshore habitat while lactating, females fed exclusively in the slope habitat and made deeper and longer dives in the postlactation period (dive depth, χ^2 = 396.8, $\chi^2_{0.05;[5]}$ = 11.070, p < 0.001; dive duration, χ^2 = 168.4, $\chi^2_{0.05;[5]}$ = 11.070, p < 0.001).

Discussion

During the nonbreeding season, lactating California sea lions showed significant individual variability in most of their foraging behaviors. Even so, annual differences were detected and likely reflected a behavioral response to El Niño conditions. Most lactating females fed exclusively in the offshore habitat, traveled farther from the colony, spent more time traveling on foraging trips, and spent more time in transit from the foraging areas to the colony during the 1993 El Niño. Females also made deeper and longer dives, and had fewer dive bouts and fewer dives per bout during the 1993 El Niño than during the non-El Niño conditions in 1996. The results suggest that California sea lion prey were concentrated in the offshore habitat and located farther from the colony and deeper in the water column during the 1993 El Niño. Although females altered their foraging behavior during El Niño, the early termination of lactation in 1993 suggests that many females did not obtain enough food to support the energetic cost of lactation, consequently they weaned their pups early or their pups died before weaning. DeLong and Melin (2000) reported a high rate of mortality of pups born in 1992 and poor condition of 4-month-old

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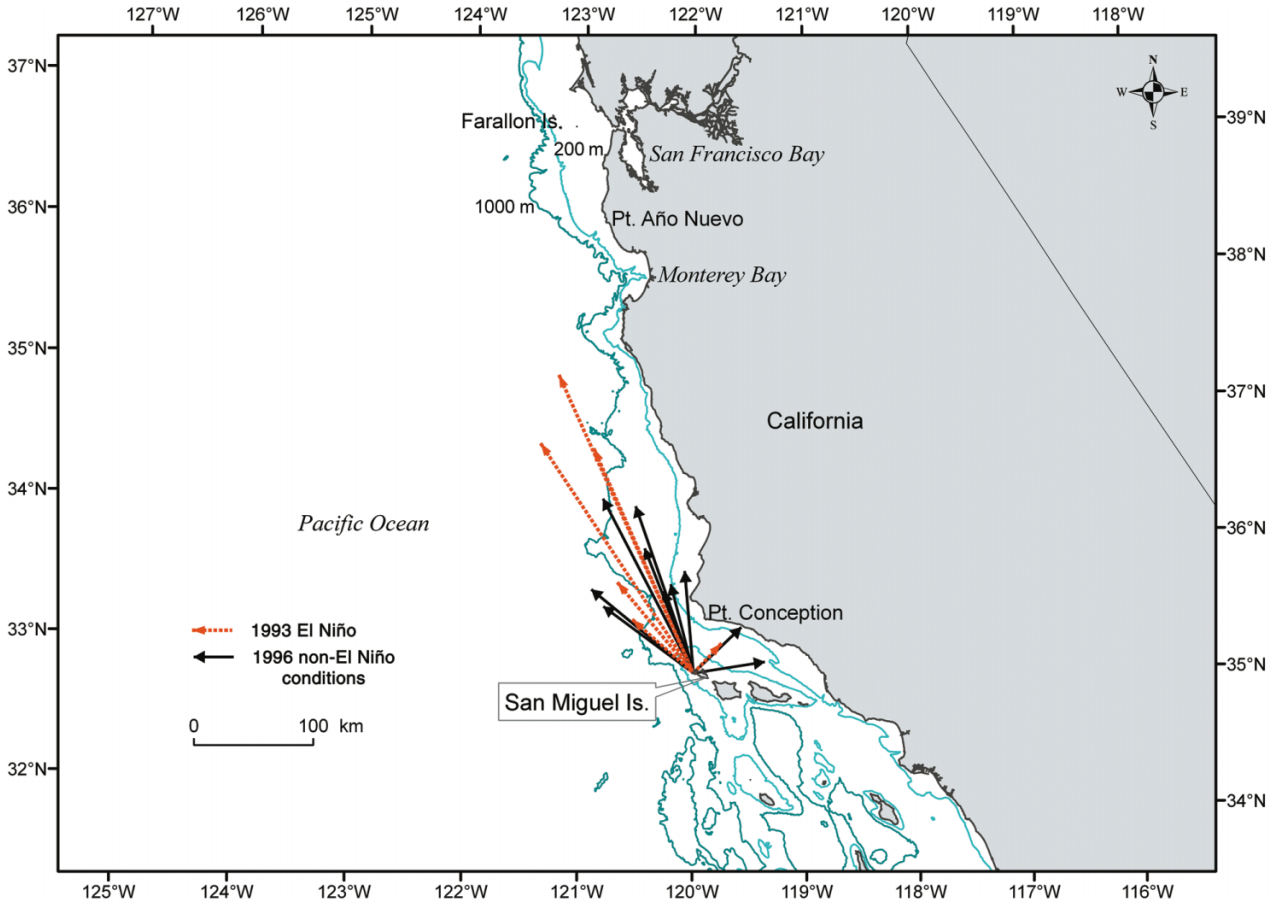
Fig. 2. Vectors depicting the mean direction and distance that lactating California sea lions (*Zalopus californianus californianus*) traveled during multiple foraging trips from San Miguel Island, California, in the nonbreeding seasons during the 1993 El Niño (n = 6) and 1996 non-El Niño (n = 10) oceanographic conditions.



pups at San Miguel Island in the fall of 1992. Because El Niño conditions persisted through the winter and spring of 1993, it is unlikely that pups would have reached weaning condition early. It is more likely that they died before they were weaned.

Juvenile Pacific hake, California market squid, rockfishes, jack mackerel, Pacific mackerel, Pacific sardine, and northern anchovy have been reported as important prey of California sea lions throughout the year (Antonelis et al. 1984; Antonelis et al. 1990; Lowry et al. 1990; DeLong et al. 1991; this study). DeLong et al. (1991) reported a significant shift in the relative proportions of primary prey species and the occurrence of new prey items in the breeding-season diet of California sea lions during the 1982–1983 El Niño. We also found that the relative proportions of the primary prey in El Niño and non-El Niño conditions were different. However, with the exception of northern anchovy occurring only in 1996, we found that the prey species that female California sea lions consumed did not change significantly between El Niño and non-El Niño conditions. The increase in the occurrence of Pacific sardine, northern anchovy, and California market squid in the diet likely reflects the increase in abundance of these species in 1996 compared with 1993 as a result of colder, more productive oceanographic conditions in 1996 (California Department of Fish and Game 1997; Schwing et al. 1997). However, the emergence of Pacific sardine as a primary prey for sea lions at San Miguel Island is a new finding. The occurrence of this prey species in the diet likely reflects its increased availability in the 1990s as the sardine population recovered from overfishing in the 1940s (California Department of Fish and Game 2000).

While lactating California sea lions showed flexibility in many of the distribution and diving parameters that we measured during the nonbreeding season, trip duration and most of the activity parameters (transit time to the first feeding bout, percentage of time spent bout-diving, and the percentage of time spent swimming and resting (interbout time)) did not change significantly during the 1993 El Niño. The mean percentage of time females spent bout-diving (44.6% in 1993, 50.2% in 1996) was greater than reported for the breeding season in the 1980s (32.7%; Feldkamp et al. 1989) and the percentage of time swimming and resting was less (37.3% in 1993, 39.3% in 1996; 44.5% (Feldkamp et al. 1989). Travel time was less in 1993 (10.5%) than breeding-season travel time in the 1980s (16.5%; Feldkamp et al. 1989) but travel time in 1996 was similar (18.1%). The mean time spent bout-diving for female California sea lions at San Miguel Island during the nonbreeding season was similar to mean values reported for females at San Nicolas Island (41.5%; Kuhn 2006) and for other sea lion species (52.7% for New Zealand sea lions (*Phocarctos hookeri* (Gray, 1844)) (Chilvers et al. 2006); 52.7% for South Amer-

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Table 4. Foraging distribution, trip activity, and diving behavior of lactating California sea lions (*Zalopus californianus californianus*) at San Miguel Island, California, between January and May in 1993 and 1996.

	1993 El Niño			1996 non-El Niño conditions			*p*	
	No. of females	No. of trips	Mean ± SE	No. of females	No. of trips	Mean ± SE	Between years	Within year
Distribution								
Distance from colony (km)	6	50	161.0±8.2	10	87	101.2±5.6	0.001	0.001
Distance from coast (km)	6	50	60.7±4.5	10	87	44.1±3.1	0.001	0.001
Activity pattern								
Trip duration (h)	3	10	116.0±17.5	6	49	135.8±7.9	0.307	0.035
Percent time spent bout-diving	3	10	44.6±3.0	6	49	50.2±1.4	0.108	0.001
Percent time between bouts	3	10	37.3±2.9	6	49	39.3±1.3	0.356	0.001
Percent time traveling	3	10	18.1±2.3	6	49	10.5±1.0	0.005	0.860
Transit time outbound (h)	3	10	8.5±1.7	6	49	5.7±0.8	0.139	0.166
Transit time inbound (h)	3	10	13.9±2.2	6	49	7.9±1.0	0.017	0.018
No. of dives/h per trip	3	10	3.6±0.6	6	49	7.2±0.3	0.001	0.003
Diving behavior								
Duration (min)	3	10	5.0±0.3	6	49	2.5±0.1	0.001	0.001
Depth (m)	3	10	194.2±11.1	6	49	70.2±4.9	0.001	0.001
Daytime depth (m)	3	10	212.8±21.6	6	49	92.8±8.0	0.001	0.001
Nighttime depth (m)	3	10	180.4±21.7	6	49	56.7±8.1	0.001	0.001
Diving effort								
No. of bouts/trip	3	10	11.9±2.6	6	49	19.4±1.2	0.012	0.029
Bout duration (h)	3	10	4.7±0.6	6	49	3.4±0.3	0.057	0.001
No. of dives/h per bout	3	10	8.5±0.8	6	49	14.5±0.4	0.001	0.001
Interbout time (h)	3	10	4.1±0.4	6	49	3.2±0.2	0.057	0.001

Note: Distribution parameters were calculated for all females for which satellite positions were available. Activity and diving statistics are summarized from TDRs.

ican sea lions (*Otaria flavescens* (Shaw, 1800)) (Werner and Campagna 1995); 57.9% for Australian sea lions (*Neophoca cinerea* (Péron, 1816)) (Costa and Gales 2003)).

In our study, lactating California sea lions fed mostly in the epipelagic zone (the upper 200 m of the water column) but many females dove to depths exceeding 400 m and the deepest dive was greater than 482 m in both years. Such deep diving has not been previously reported for California sea lions and has only been reported for one other otariid, the New Zealand sea lion (Costa and Gales 2000). Although they have the ability to travel 300 km from the colony on a single foraging trip and to dive to depths in excess of 482 m, lactating California sea lions do not dive to the maximum depths or travel the maximum distances regularly. Presumably, extreme behaviors are energetically costly and are only employed when necessary because of a redistribution or reduction of prey (Costa et al. 2001), as often occurs during El Niño events.

California sea lions at San Miguel Island appear to have two modes of foraging behavior that probably evolved in response to seasonal distribution of their prey. During the 3-month summer breeding season, prey are located close to the colony and concentrated over the continental shelf (Antonelis et al. 1990) and females are constrained in trip duration by the need to nurse a dependent pup. Consequently, lactating females make short trips (2–3 days) and feed mostly over the continental shelf (Feldkamp et al. 1989; Antonelis et al. 1990; Melin and DeLong 2000). They are shallow bout-divers, generally not diving deeper than 80 m, and most females show pronounced diel diving behavior, as they follow their prey from deep depths during the day to shallow depths at night. Based on our findings and those of Melin and DeLong (2000), a transformation in feeding behavior takes place between the breeding and nonbreeding season that is driven by a less constrained attendance pattern (the pup becomes more independent and begins supplementing its diet by 6 months of age) (Melin et al. 2000) and the dispersal of prey into offshore habitats and to greater depths (Fields 1965; Bailey et al. 1982; MacCall and Stauffer 1983; Larson et al. 1994; Sakuma and Ralston 1997; Schwartzlose et al. 1999). Females show a greater range of feeding behaviors: they extend their foraging trips (4–5 days) (Melin et al. 2000), occupy the shelf, slope, and offshore habitats, dive over a greater range of depths (maximum >482 m), and expend greater diving effort (mean bout length 3.4 h; mean interbout interval 3.2 h). Other otariids that have lactation periods similar to or longer than those of California sea lions (6 months to 2 years) show a similar progression from constrained to more varied feeding behavior in response to seasonal changes in prey distribution and the pup becoming more independent (Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) (Merrick and Loughlin 1997), Australian sea lions (Costa and Gales 2003), Juan Fernández fur seals (*Arctocephalus philippii* (Peters, 1866)) (Francis et al. 1998), New Zealand fur seals (*Arctocephalus forsteri* (Lesson, 1828)) (Mattlin et al. 1998), Australian fur seals (*Arctocephalus pusillus doriferus* Wood Jones, 1925) (Arnould and Hindell 2001), and subantarctic fur seals (*Arctocephalus tropicalis* (J. E. Gray, 1872)) (Georges et al. 2000)).

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Fig. 3. Distribution of dive depths of lactating California sea lions (*Zalopus californianus californianus*) determined from SLTDR data. Females were instrumented at San Miguel Island, California, in the nonbreeding seasons during the 1993 El Niño (n = 6) and the 1996 non-El Niño (n = 9) oceanographic conditions. Error is +1 SE.

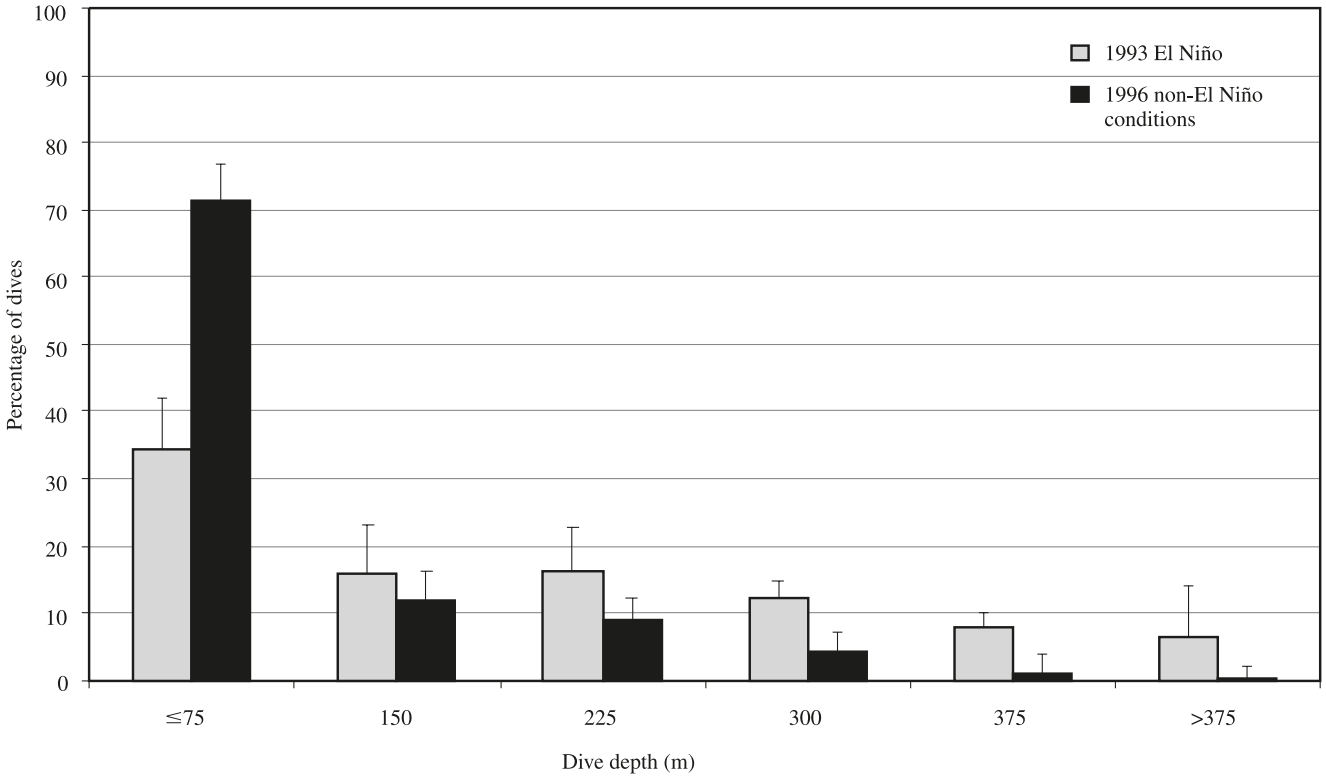

Fig. 4. Distribution of dive durations of lactating California sea lions (*Zalopus californianus californianus*) determined from SLTDR data. Females were instrumented at San Miguel Island, California, in the nonbreeding seasons during the 1993 El Niño (n = 6) and the 1996 non-El Niño (n = 9) oceanographic conditions. Error is +1 SE.

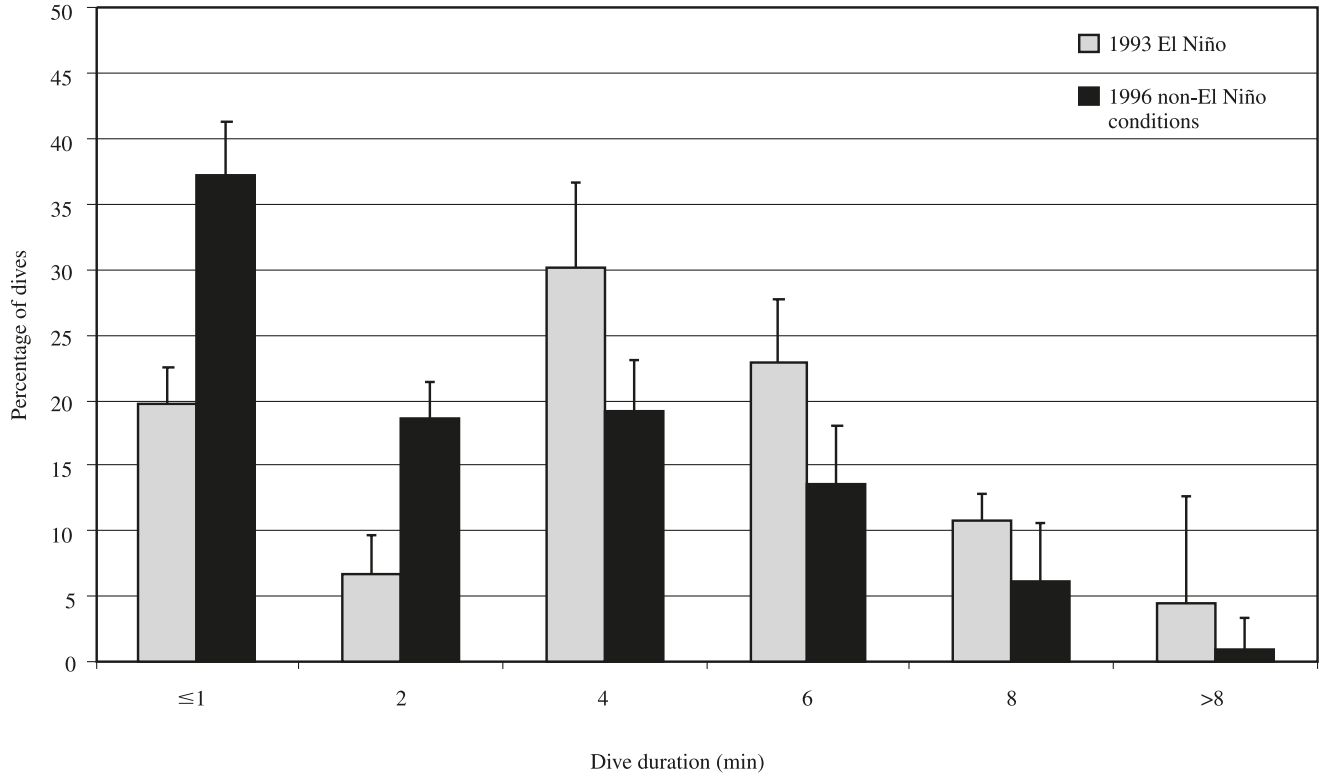

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Table 5. Foraging-behavior parameters for individual lactating California sea lions (*Zalopus californianus californianus*) at San Miguel Island, California, between January and May in 1993 and 1996.

	1993 El Niño			1996 non-El Niño conditions					
	93044	93302	93395	96202	96532	96553	96633	96673	96714
Activity pattern									
Number of trips	2	6	2	14	6	14	5	6	4
Trip duration (h)	191.9±34.7	52.5±20.0	103.8±24.5	124.4±13.0	128.5±19.8	158.0±13.0	138.6±21.7	123.3±19.8	141.8±24.3
Percent time bout-diving	31.6±6.0	61.1±3.5	41.0±6.0	57.1±2.3	42.4±3.5	53.0±2.3	55.1±3.8	57.7±3.5	35.7±4.2
Percent time between bouts	50.0±5.7	20.8±3.3	41.2±5.7	33.1±2.2	43.8±3.3	35.5±2.2	36.7±3.6	32.7±3.3	54.1±4.0
Percent time traveling	18.4±4.5	18.1±2.6	17.8±4.5	9.9±1.7	13.8±2.6	11.5±1.7	8.2±2.8	9.6±2.6	10.2±3.2
Transit time outbound (h)	14.6±3.3	2.9±1.9	8.1±3.3	4.4±1.3	5.7±1.9	5.8±1.3	6.3±2.1	5.7±1.9	6.6±2.4
Transit time inbound (h)	20.4±4.1	5.3±1.4	16.0±2.9	7.0±1.7	10.4±2.5	11.8±1.7	4.7±2.8	6.1±2.5	7.2±3.1
No. of dives/h per trip	3.7±1.2	2.9±0.7	4.1±1.2	6.4±4.7	7.2±0.7	7.5±0.5	8.3±0.8	9.5±0.7	4.4±0.9
Diving behavior									
Duration (min)	3.5±0.5	8.1±0.3	3.3±0.5	3.7±0.2	1.8±0.3	2.5±0.2	1.6±0.3	2.3±0.3	3.41±0.4
Depth (m)	121.9±21.7	334.4±12.6	126.3±21.7	109.6±8.2	46.2±12.6	83.5±8.2	18.4±13.8	72.7±12.6	91.1±15.4
Daytime depth (m)	143.3±50.2	331.7±20.5	163.3±35.5	109.0±13.4	110.0±20.5	144.8±13.4	23.3±22.4	76.9±20.5	92.8±25.1
Nighttime depth (m)	103.4±35.6	383.8±20.6	53.8±50.4	99.3±13.5	23.9±20.6	57.6±13.5	12.3±22.5	54.2±20.6	92.7±25.2
Diving effort									
No.of bouts/trip	17.5±5.1	4.8±2.9	13.5±5.1	15.7±1.9	20.3±3.0	23.3±1.9	24.2±3.2	17.0±2.9	15.5±3.6
Bout duration (h)	3.4±1.2	7.9±0.7	2.8±1.2	4.6±0.5	2.8±0.7	3.6±0.5	1.8±0.8	4.5±0.7	3.1±0.8
Dives/h per bout	12.0±1.6	4.6±0.9	9.1±1.6	10.5±0.6	15.5±0.9	12.3±0.6	22.4±1.0	16.5±0.9	9.8±1.2
Interbout time (h)	5.6±0.8	3.5±0.5	3.2±0.8	3.0±0.3	2.9±0.5	2.6±0.3	2.3±0.5	2.8±0.5	5.5±0.6

Note: Data are summarized from TDRs. Values are given as the mean ± 1 SE.

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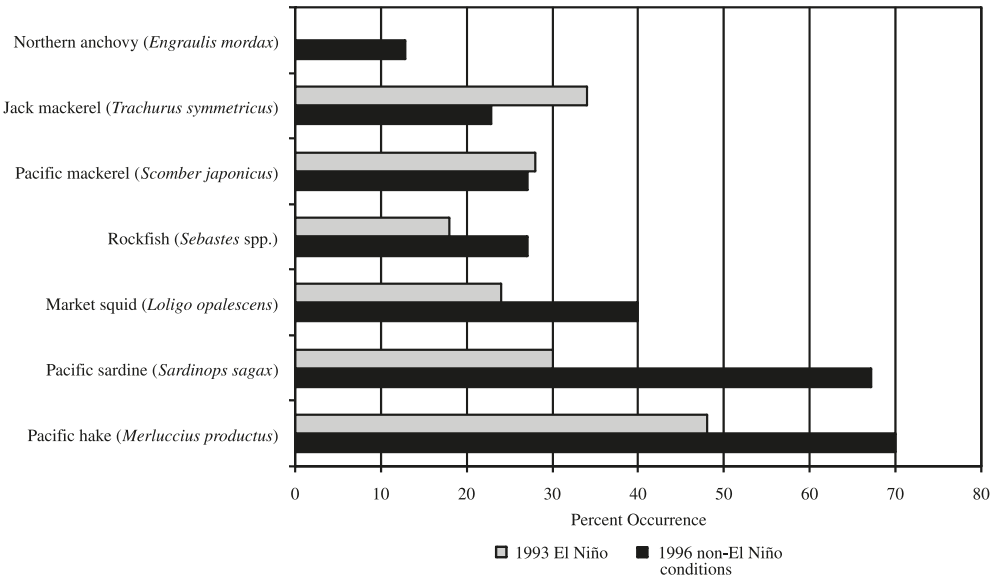
Fig. 5. Percent occurrence of prey species determined from hard parts recovered in scats that were collected from California sea lion (*Zalopus californianus californianus*) haul-out areas on San Miguel Island, California, in March and May during the1993 El Niño (n = 50) and 1996 non-El Niño (n = 70) oceanographic conditions.



As in previous foraging studies of lactating California sea lions at San Miguel Island, we found that females fed primarily northwest of the island (Antonelis et al. 1990; Melin and DeLong 2000). Even during El Niño, when prey were distributed farther north, females did not change the direction they traveled for feeding. This suggests that females have fidelity to feeding areas northwest of San Miguel Island. Robson et al. (2004) found that lactating northern fur seals (*Callorhinus ursinus* (L., 1758)) at St. Paul and St. George islands in the Bering Sea (approximately 67 km apart) showed fidelity to foraging areas that were associated with their breeding island. Fidelity to feeding areas by geographic subpopulations of sea lions is likely related to seasonal predictability of prey fields but would benefit lactating females by reducing intraspecific competition for food among nonmigratory lactating females that do not have the option to travel to foraging grounds farther from the colonies. Indeed, partitioning of food resources may be particularly important during the nonbreeding season or during El Niño conditions if prey are more dispersed or less abundant near the breeding colonies. The two largest populations of breeding California sea lions (~100 000 animals at each colony) are at San Miguel Island and at San Nicolas Island, 120 km southeast of San Miguel Island. A recent study of the foraging distribution of lactating females at San Nicolas Island indicated some overlap between the San Nicolas and San Miguel populations, but most of the females from San Nicolas Island fed in areas southeast of the island (Kuhn 2006). Thus, it appears that the two largest populations of lactating sea lions feed in different geographic areas and on different prey resources during the nonbreeding season. However, instrumentation of females at both colonies was confined to the north end of each island, and the lack of overlap may reflect fine-scale fidelity to feeding areas, based on the location of the female in the colony, as reported for northern fur seals (Robson et al. 2004) (e.g., a female instrumented at the north end of the island feeds to the north of it, while a female instrumented at the south end of the colony feeds to the south). To determine the degree of overlap of foraging areas at the two colonies, additional studies at different breeding areas at both islands need to be conducted (e.g., a south rookery on San Nicolas Island and a southeast rookery on San Miguel Island).

During the 1993 El Niño, the primary differences in foraging behavior before and after lactation were that females commuted from haul-out sites along the coast and fed closer to the California coast during the postlactation period. Females exploited the same range of dive depths but a greater percentage of the dives were deeper and longer during the postlactation period. The increase in deeper diving suggests that females were targeting prey located deeper in the water column and presumably of sufficient energetic value to offset the cost of deeper diving (Costa et al. 2001). The shift to deeper diving may reflect the ability of females to expend more energy diving when they are not supporting a dependent pup. Whether the behavioral changes before and after lactation observed in this study are characteristic of female California sea lions is unclear. Because the data were available only for females during El Niño conditions, the observed behaviors may represent a shift in behavior that was forced by a redistribution of prey northward and deeper in the water column in 1993. However, one advantage of foraging from haul-out sites closer to feeding areas is that females may spend more time feeding than traveling during a foraging trip, potentially increasing their energy gain per trip. Significant gains in energy assimilation shortly before giving birth would likely increase the chance of survival of the new pup.

The nonbreeding season represents 66% of the time invested by a lactating California sea lion in her pup and all of the time invested in her pregnancy. Therefore, her behavior during this time has ramifications for her current and future reproductive success and plays an important role in driving population trends. The results from this study sug-

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gest that the diverse diet and the behavioral capabilities of lactating California sea lions provide many foraging options during periods of redistribution or reduction of food. Such flexibility in behavior has likely contributed to the successful recovery of the population over the past 35 years despite oceanographic changes in the California Current that caused the decline of many populations of marine species (Hayward et al. 1999).

Acknowledgements

We thank all the biologists who assisted in handling animals in the field, and J. Griffith, B. Hanson, and J. Thomason, who processed and identified scat contents. The staff members at Channel Islands National Park and Channel Islands Aviation provided logistical support. P. Gearin, R. Ream, G. Duker, K. Ono, and an anonymous reviewer reviewed the manuscript. This study was funded by NOAA, National Marine Fisheries Service, Alaska Fisheries Science Center, National Marine Mammal Laboratory; University of California, Santa Cruz, California, and the Office of Naval Research, Washington, D.C. Fieldwork was conducted under Marine Mammal Protection Act Permit Nos. 717 and 977 issued to the National Marine Mammal Laboratory.

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