ABSTRACT

The at-sea distribution and diving behavior of lactating California sea lions at San Miguel Island were studied during the breeding and non-breeding seasons in 1995 to 1996. Satellite Linked Time-Depth Recorders (SLTDRs) were used to obtain at-sea locations and diving information during foraging trips. A total of 90 and 346 at-sea locations were recorded during the breeding and non-breeding seasons, respectively. Females foraged along the California coast, some traveling as far north as Monterey Bay and offshore to the 1,000-m isobath; 72.2% and 66.8% of all at-sea locations were northwest of San Miguel Island in the breeding and non-breeding seasons, respectively. In both seasons, more than 80% of the at-sea locations were less than 150 km from San Miguel Island. During the non-breeding season, most locations (67.0%) were over the slope or offshore; during the breeding season, most locations (63.6%) were over the continental shelf. Dives were shallow, <75 m, and of short duration, <4 min. Females dived deeper and dives were longer in the 1995 to 1996 non-breeding season than during the breeding season. The seasonal differences in foraging behavior of lactating California sea lion females are probably due to seasonal changes in prey availability and the stage of lactation of the female.

Keywords: *Zalophus californianus*, non-breeding season, breeding season, foraging behavior, satellite telemetry, lactating.

INTRODUCTION

Four species of pinniped breed on the California Channel Islands: the harbor seal (*Phoca vitulina*), northern elephant seal (*Mirounga angustirostris*), northern fur seal (*Callorhinus ursinus*), and California sea lion (*Zalophus californianus*). How these species partition the food and space resources of the California Current ecosystem has been the focus of research at the California Channel Islands since the 1970s (Antonelis and Fiscus 1980; Stewart et al. 1993; DeLong and Melin 1999, this volume; Stewart and Yochem 1999, this volume). The annual cycle and foraging ecology of northern elephant seals (DeLong and Stewart 1991; DeLong et al. 1992; Stewart and DeLong 1995) and harbor seals at San Miguel and San Nicolas Islands (Stewart and Yochem 1994) have been described in detail as a result of this research effort. Other than a study in 1985 comparing the at-sea distributions of northern fur seals and California sea lions during the breeding season (Antonelis et al. 1990), the annual patterns of at-sea distribution and diving behavior of northern fur seals and California sea lions remain relatively unknown. It is likely, however, that the at-sea distribution and diving behavior for these species change throughout the year because during the lactation period, lactating females may have to adjust their feeding behavior to accommodate seasonal changes in prey distribution (Antonelis et al. 1984, 1990; Lowry et al. 1990, 1991) and increasing energetic demands of the pups (Gentry and Holt 1986; Ofstedal et al. 1987). The objective of this paper is to provide a general description of the annual pattern of the at-sea distribution and diving behavior of lactating female California sea lions at San Miguel Island.

The behavior of California sea lions during the breeding season has been described in detail (Peterson and Bartholomew 1967; Odell 1972; Heath 1989; Antonelis et al. 1990). The pupping and breeding season occurs during the summer months from May through July each year. Adult females at San Miguel Island give birth to pups in May and June, and breed during July. During this time, females alternate 3-d foraging trips at-sea with 2-d nursing visits on land (Antonelis et al. 1990). Once the breeding season ends, adult males and many juveniles disperse northward, but lactating females remain at San Miguel Island and continue to nurse their pups during the non-breeding season for 6 to 11 mo (Melin 1995). In a four-year study of attendance patterns during the last 6 mo of the lactation period, Melin (1995) reported that foraging trips lasted an average of 3.4 to 4.6 d and nursing visits lasted an average of 1.2 to 1.3 d.

During foraging trips in the breeding season, California sea lion females feed over the continental shelf and travel an average of 54.2 km from San Miguel Island. A study of diving behavior of females during the breeding season found that most dives were less than 80 m, and dive durations were less than 3 min (Feldkamp et al. 1989). Thus, during the breeding season, females are primarily coastal foragers and shallow divers.
dive duration bins were defined as 76 to 150, 151 to 225, 226 to 300, 301 to 375, and >375 m; corder was 4 m. Dive depth bins were defined as >8 to 75, ered a dive was >8 m, and the depth resolution of the re- samples every 30 s, the minimum dive depth to be consid- grams in pre-defined depth and duration bins. Depth was data collected by the SLTDRs were summarized as histo- dur 4 m. Dive depth bins were defined as >8 to 75, 76 to 150, 151 to 225, 226 to 300, 301 to 375, and >375 m; dive duration bins were defined as #2, >2 to 4, >4 to 6, >6 to 8, and >8 min. The details of how locations are determined and loca- tion qualities from SLTDRs has been described in detail else- where (Harris et al. 1990; Frost and Lowry 1994; Service Argos Incorporated 1996). Locations were classified as Z, B, A, 0, 1, 2, and 3, indicating poor to good quality locations (Service Argos Incorporated 1996). SLTDR locations rated ‘Z’ quality by the processing center were discarded because they were unreliable. Most locations were class 0, A, or B which were evaluated on a point-by-point basis, using a maximum swim speed of 10 km/hr (Feldkamp et al. 1989) and the elapsed time between consecutive points, to determine whether the location was accepted (Frost and Lowry 1994; Merrick and Loughlin 1997). The distribution of foraging locations relative to direction from San Miguel Island was determined by using the fixed latitude and longitude for the rookery at the west end of San Miguel Island (34°01’ N, 120°26’ W) as the center and creating a four-cell grid. This created northwest, northeast, southeast and south- west quadrants which were used to classify the direction of foraging from San Miguel Island. The outer boundaries of each quadrant were determined by the coastline or by three degrees latitude or longitude from the center. The quadrants were not equal in size because of the curve of the coastline. The distance of each location from San Miguel Island was calculated and then allocated to one of five distance bins: #50, 51 to 100, 101 to 150, 151 to 200, and >200 km. These data were used to describe the range of distances females foraged from San Miguel Island. We calculated percentages of the distance and direction from San Miguel Island and inshore-offshore distribution of California sea lions from data presented in Antonelis et al. (1990) for an historical comparison with our results. In Antonelis et al. (1990), nine California sea lion females were instrumented with VHF radio transmitters and line-transect aerial surveys were flown to locate the animals at sea. We calculated percentages from tables contained in the paper. SLTDR diving data were analyzed by summing the counts of dives in each depth and duration bin for all fe- males in each year. Statistical tests were conducted with al- pha=0.10.

RESULTS

Foraging Locations

At-sea locations were obtained for six females in the breeding season and ten females in the non-breeding sea- son. Females foraged northwest of San Miguel Island in waters over the continental shelf, continental slope and in the pelagic zones in both seasons (Figure 1). All quadrants were used by the animals, but the southwest quadrant was not used during the breeding season (Table 1). During the study period, 72.2 and 66.8% of the locations were in the northwest quadrant in the breeding and non-breeding seas- ons, respectively (Table 1). The percentage of locations in the northwest quadrant was similar between the two seasons (χ^2=26.976; p<0.001). In both seasons, the per- centage of locations in the northwest quadrant was greater than all other quadrants (breeding season: d.f.=1; χ^2=17.689; p<0.001; non-breeding season: d.f.=1; χ^2=38.823; p<0.001). During the breeding season, most of the locations (63.6%; n=90) occurred in waters over the continental shelf and shelf break (<200 m isobath). During the non-breeding season, most of the locations (67.0%; n=346) occurred over the shelf slope and in offshore pelagic waters. A significantly greater percentage of locations occurred in offshore pelagic waters in the non-breeding season than in the breeding season (d.f.=1; χ^2=26.976; p<0.001). Most locations in the breeding (84.5%) and non-breeding (81.2%) seasons occurred at distances less than 150 km from San Miguel Island (Table 1). A higher percentage of locations occurred at distances less than 100 km during the non-breeding season (57.2%) compared to the breeding sea- son (42.3%) (d.f.=1; χ^2=5.885; p<0.001). However, a higher percentage of locations also occurred at distances greater than 200 km during the non-breeding season (10.7%) com- pared to the breeding season (2.2%) (d.f.=1; χ^2=5.296; p<0.001). In the Antonelis et al. (1990) study, 55% of the at-sea locations (n=16) of California sea lions were northwest of San Miguel Island, 56% were less than 50 km from San Miguel Island, and 81.3% occurred over the continental shelf or shelf break (or the shelf waters surrounding San Miguel and Santa Rosa Islands). The percentages of locations north- west of San Miguel and over the continental shelf were simi- lar to the percentages in the 1995 breeding season.
Table 1. Distribution of at-sea locations of California sea lion females from San Miguel Island during the breeding and non-breeding seasons in 1995-96. Quadrants are described as: >34°01’ N, >120°26’ W = Northwest; >34°01’ N, ≤120°26’ W = Northeast; ≤34°01’ N, ≤120°26’ W = Southeast; ≤34°01’ N, >120°26’ W = Southwest. Distances are determined using San Miguel Island (34°01’ N, 120°26’ W) as the center of a circle with concentric circles at 50 km intervals from the center.

<table>
<thead>
<tr>
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<th>Number of females*</th>
<th>Number of locations</th>
<th>Percent of Locations by Direction</th>
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<td></td>
<td></td>
<td></td>
<td>Northwest</td>
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<tr>
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<td>72.2</td>
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<tr>
<td>Non-breeding</td>
<td>10</td>
<td>346</td>
<td>66.8</td>
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</table>

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<table>
<thead>
<tr>
<th></th>
<th>Number of females*</th>
<th>Number of locations</th>
<th>Percent of Locations by Distance (km)</th>
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<tbody>
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<td></td>
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<td>&lt;=50</td>
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<tr>
<td>Breeding</td>
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<td>Non-breeding</td>
<td>10</td>
<td>346</td>
<td>23.7</td>
</tr>
</tbody>
</table>

*Number of females for non-breeding season includes: 4 females with locations for both seasons, 2 females with locations for the winter only, and 4 females with locations for the spring only.

(direction: d.f.=1; \( \chi^2=0.783; \ p=0.100 \); inshore: d.f.=1; \( \chi^2=0.000; \ p=0.100 \)), but the percentage of locations greater than 100 km from San Miguel was significantly less than that during the 1995 breeding season (d.f.=1; \( \chi^2=12.441; \ p<0.001 \)).

Diving Behavior

Histogram dive data were recovered from all females for which locations were obtained. In the 1995 to 1996 breeding season, 96% of all dives were between 8 and 75 m and 92% of all dives were less than 4 min in duration (Figures 2 and 3). In the non-breeding season, 77% of the dives were between 8 and 75 m and 81% of the dives were 4 min or less in duration. Dive depth bins were collapsed into two categories for seasonal comparisons: shallow (8 to 75 m) and deep (>75 m). Dive duration bins were collapsed into short (up to 4 min) and long (>4 min) duration. Females dived deeper (\( \chi^2=3092.3; \ p<0.001 \)) and had longer dives (\( \chi^2=2935.4; \ p<0.001 \)) in the non-breeding season than in the breeding season.

DISCUSSION

The results presented here indicate that the at-sea distribution and diving behavior of lactating California sea lions from San Miguel Island changed during different phases...
of the reproductive cycle. During the breeding season, females foraged more than 100 km from San Miguel Island over the continental shelf and dived to shallow depths whereas during the non-breeding season, the distribution was less than 100 km from San Miguel Island in offshore pelagic waters and the diving was deeper. In the Antonelis et al. (1990) study and both seasons in this study, lactating females preferred the northwest quadrant, suggesting that this geographic region (as defined here) is important to California sea lions year round. The continental shelf habitat was most important to females during the breeding season in both 1985 and 1995, indicating that this habitat contained preferred prey assemblages during the breeding season. However, females foraged farther from San Miguel Island during the breeding season in 1995 than in 1985. This difference suggests that females traveled farther to feed in 1995 than they did 10 years earlier. During the 10 years between the two studies, the population of California sea lions increased by 71% or more (Barlow et al. 1997). It is feasible that more females have been exploiting the continental shelf habitat during the breeding season and, consequently, the foraging range of lactating females during the breeding season has expanded farther north along the continental shelf as a density-dependent response to population growth. However, the difference could also result from different study methods and small sample sizes (16 locations for nine females in the Antonelis et al. [1990] study; 90 locations for six females in this study) or from inter-annual variability in the distribution of prey.

The food habits of California sea lions during the breeding and non-breeding seasons are different and are influenced by the spatial and temporal availability and abundance of different prey types (Antonelis et al. 1984; Lowry et al. 1990; Lowry et al. 1991). The non-breeding season appears to be a time when prey is available over a greater variety of marine habitats and/or was more dispersed. The change in modal foraging distance from between 100 and 200 km to less than 100 km between the breeding and non-breeding season in 1995 to 1996 was surprising. It was expected that if there were differences in distance to foraging areas between seasons, females would forage closer to San Miguel Island (about 50 km) during the breeding season. During this time, the pups are nutritionally dependent on the female, and females reportedly have short absences from the rookery (3 d; Antonelis et al. 1990) which would restrict the travel distance of females. During the non-breeding season, pups are probably supplementing their milk diets by foraging close to San Miguel Island, and females are reportedly absent from the rookery longer periods (3.4 to 4.3 d; Melin 1995) which would allow them to travel farther on foraging trips. In this study, females traveled shorter distances, suggesting that
longer foraging trips observed by Melin (1995) may be indicative of more time spent searching for prey, perhaps because prey is more patchily distributed over a greater variety of marine habitats during the winter and spring. Although the longer foraging trips could reflect changes in foraging behavior to meet increased energetic demands of the pup as it grows (Gentry and Holt 1986; Ofstedal et al. 1987), Melin (1995) suggested that California sea lions met this demand by changing feeding behavior during foraging trips rather than by changing their foraging trip lengths during the last 6 mo of the lactation period. Thus, the difference in modal foraging distance between the breeding and non-breeding seasons appears to be related to increased searching time and seasonal changes in prey distribution.

The shallow dives and short dive durations observed during the breeding season in this study are similar to those reported by Feldkamp et al. (1989) and agree with food-habit information (Antonelis et al. 1984; Lowry et al. 1990; Lowry et al. 1991), indicating that California sea lions feed at shallow depths. During the non-breeding season in this study, females dived deeper and longer than during the breeding season, but more than 70% of the dives were shallow and of short duration. This pattern indicates that while females were foraging offshore in deeper water during the non-breeding season, they still fed predominately at shallow depths. Consequently, whether females are foraging over the continental shelf, the shelf slope, or in pelagic water, they are feeding on prey assemblages associated with the upper 75 m of the water column.

The results of this study indicate that lactating California sea lions are year-round residents of San Miguel Island and that they utilize primarily the coastal and offshore waters northwest of San Miguel Island from Point Conception to Monterey Bay for feeding. Whether the change in the foraging behavior of lactating females over the past 10 years is a density-dependent response to the growing population or is within the bounds of inter-annual variability in prey distribution requires further study.

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LITERATURE CITED


Melin, S. R. and R. L. DeLong


