



Notes

MARINE MAMMAL SCIENCE, 34(1): 238–249 (January 2018)

© 2017 Society for Marine Mammalogy

DOI: 10.1111/mms.12449

Movements and dive behavior of juvenile California sea lions from Año Nuevo Island

ELIZABETH A. MCHURON,¹ Department of Ecology and Evolutionary Biology, University of California Santa Cruz, 115 McAllister Way, Santa Cruz, California 95060, U.S.A.; BARBARA A. BLOCK, Department of Biology, Stanford University, Hopkins Marine Station, 120 Ocean View Boulevard, Pacific Grove, California 93950, U.S.A.; DANIEL P. COSTA, Department of Ecology and Evolutionary Biology, University of California Santa Cruz, 115 McAllister Way, Santa Cruz, California 95060, U.S.A.

Studies on the movements and foraging behavior of marine mammals have become relatively commonplace with recent advancements in bio-logging technology, but even for well-studied species there is often a strong bias towards particular demographic groups (Hazen *et al.* 2012). For otariids, electronic tagging and tracking studies are often focused on adult females because of their influence on population dynamics, and because their life history characteristics and size facilitate instrument recovery and handling compared with other demographic groups. To date, there have been comparatively few studies on the movements and foraging behavior of juvenile otariids despite the need for knowledge of this critical life history stage (Loughlin *et al.* 2003; Raum-Suryan *et al.* 2004; Fowler *et al.* 2006; Jeglinski *et al.* 2012, 2013; Hückstädt *et al.* 2014; Leung *et al.* 2014; Baylis *et al.* 2017). Juvenile otariids may not exhibit the same foraging behavior as reproductively mature adults because of differing energetic needs, life history constraints, lack of experience, or physiological and morphological limitations (Horning and Trillmich 1997; Fowler *et al.* 2006; Jeglinski *et al.* 2012, 2013; Leung *et al.* 2014). These limitations may restrict the amount of foraging habitat available to juveniles, and may contribute to decreased foraging success and high mortality during periods of reduced prey availability, such as El Niño events (Trillmich and Limberger 1985, Trillmich *et al.* 1991).

California sea lions (*Zalophus californianus*) are the most abundant otariid inhabiting the California Current Ecosystem, with an estimated population size of 297,000 individuals (Carretta *et al.* 2015). They generally forage on the continental shelf on a variety of schooling fish and cephalopods (Weise and Harvey 2008, Orr *et al.* 2011,

¹Corresponding author (e-mail: emchuron@ucsc.edu).

Melin *et al.* 2012), although adults also use offshore habitat (Weise *et al.* 2006, Melin *et al.* 2008). Sea lion prey abundance and distribution varies seasonally and annually, and is also affected by basin-scale oceanographic processes such as the El Niño Southern Oscillation and the Pacific Decadal Oscillation (Koslow *et al.* 2014, Ralston *et al.* 2015). Movements and diet are known to vary in response to these fluctuations in prey availability (Weise *et al.* 2006; Weise and Harvey 2008; Melin *et al.* 2008, 2012), with reduced prey availability adversely affecting pup growth and survival (Ono *et al.* 1987, Melin *et al.* 2012, McClatchie *et al.* 2016a). Movement data on juvenile California sea lions are limited to a single study that instrumented seven juveniles at San Miguel Island (Orr 2011, Orr *et al.* 2012), one of the largest breeding rookeries of this species (Lowry *et al.* 2017). Yearlings in this study foraged in proximity to the northern Channel Islands, whereas 2–3-yr-olds also foraged in coastal areas of southern California and west of San Francisco Bay in central California (Orr 2011). There are no published measurements of diving behavior for this demographic group, but physiological data indicate that the blood and muscle oxygen stores of juvenile sea lions are not fully developed until 1.5–2.5 yr and 4–6 yr, respectively (Weise and Costa 2007).

The objective of this study was to document movements and dive behavior of juvenile California sea lions from Año Nuevo Island, an important central California haul-out site that also supports a small breeding population (Lowry *et al.* 2017). These data were opportunistically collected during the El Niño event in 2015–2016, which was one of the strongest events on record based on tropical sea surface temperature (SST) anomalies (Jacox *et al.* 2016). The 2015–2016 El Niño event also followed a period of anomalous warming and reduced upwelling along the California coast (Zaba and Rudnick 2016, McClatchie *et al.* 2016b), allowing for possible insight into the behavior of juvenile sea lions during a prolonged period of oceanographic conditions typically associated with reduced prey availability.

Juvenile California sea lions were captured at Año Nuevo Island in October 2015 using custom hoop nets. Once captured, sea lions were manually restrained and sedated using gas anesthesia (isoflurane) administered with oxygen *via* a field portable vaporizer (Gales and Mattlin 1998). Satellite tags (SPOT 6, $n = 5$; SPLASH10F, $n = 2$; Wildlife Computers, Redmond, WA) were attached directly to the fur using 5 min epoxy (Devcon, Danvers, MA). Age was approximated in the field using standard lengths (Laake *et al.* 2016) and tooth morphology, such as the presence of milk teeth (indicative of pups) and the relative size of the canine to the incisor. Satellite tags were programmed to ensure coverage throughout the day and maximize transmission of dive data (SPOT 6, 40 transmissions/h; SPLASH10F, 900 transmissions/d), with the exception that SPOT 6 tags ceased transmissions after 4 h ashore to maximize battery life. Dive tags were programmed to transmit dive shape, maximum dive depth, and duration of individual dives, and histograms of depth and duration binned into 6 h periods. The minimum depth and duration to be considered a dive was 4 m and 16 s, criteria consistent with several papers on adult diving behavior (Kuhn and Costa 2014, McHuron *et al.* 2016).

ARGOS locations were filtered using a speed (4 m/s) and angle filter (default settings) to remove erroneous locations (R package *argosfilter*). Hourly locations were interpolated using the “best-fit” track from a continuous correlated random walk model (R package *crawl*; Johnson *et al.* 2008) that incorporates the error structure associated with all but the poorest quality ARGOS location class (Costa *et al.* 2010). We used a two-step process to identify and remove interpolated locations that occurred on land by identifying the start and end times of each trip. First, we

combined the subset of transmitted locations that had a wet/dry status message with all interpolated locations, initially assuming that interpolated locations following a status message had the same wet/dry status. Each satellite location was assigned a trip number based on the wet/dry status; a trip began when the animal departed from the haul-out and included any locations on land immediately following return from sea. Second, we calculated the distance between all locations within a trip and the first observation of the haul-out for that trip (*i.e.*, the actual transmitted message), and reclassified locations as at-sea or on land based on whether they were within 5 km of the haul-out location. For example, interpolated locations initially classified as at-sea that preceded the haul-out but were within 5 km of the haul-out location were reclassified as on land, whereas locations initially classified as on land that were greater than 5 km from the haul-out location were reclassified as at-sea and assigned to the next trip. We visually examined the final classification using ArcGIS (Version 10.2) to ensure locations classified as being on land occurred in relative proximity to haul-out locations and did not occur in directed movements towards or away from the haul-out. We calculated summary statistics of foraging trips (defined as trips lasting ≥ 6 h) and identified haul-out locations based on areas where clusters of on land locations occurred and overlapped with known sea lion haul-outs (Weise and Harvey 2008) or features used by sea lions (*e.g.*, rocky outcroppings, human structures) as identified using Google Earth Pro (Version 7.1.8).

Kernel density analyses of hourly at-sea locations were used to determine the home range (90% UD; Börger *et al.* 2006) and core area (50% UD) of all sea lions (1) during the entire tracking period, (2) by month to examine temporal changes in the size and location of home ranges and core areas, and (3) for each sea lion individually. Because sea lions differed in their total number of locations due to variation in tracking duration and time spent ashore, analyses that included multiple sea lions were weighted by individual to ensure equal contribution. We limited the monthly analysis to November, December, and January because these were the only three months where all six sea lions were tracked for the entire month, which removed the possibility that any differences in area could be attributed to differences in the number of individuals sampled. Kernel density analyses were conducted in the Geospatial Modelling Environment (Version 0.7.3.0; <http://www.spatial ecology.com/gme>) using the least squares cross validation method for the smoothing parameter. The cell size was set at 5 km to correspond to the location error associated with the mean ARGOS error of location quality "A" (Costa *et al.* 2010), as the majority (>50%) of all locations for each sea lion were of this quality or better. We used ArcGIS to calculate the mean distance of at-sea locations to the mainland coast and the 200 m isobath, and the proportion of locations on the continental shelf (within the 200 m isobath). We discuss qualitative trends in both movement and dive data but do not make any statistical comparisons given the small samples sizes. All means are presented \pm SD.

Tracking data were obtained for six of the seven sea lions. Tracking durations ranged from 127 to 243 d (Table 1) with locations that spanned southern to northern California (Fig. 1). Sea lions spent an average of 70% of the tracking duration at sea, with considerable variability among individuals (48%–83%). Foraging trips lasted an average of 1.5 ± 0.6 d followed by a haul-out period of 5.5 ± 3.4 h, but sea lions spent considerably longer in the vicinity of the haul-out before taking another foraging trip (20.5 ± 11.1 h). A total of 18 haul-out sites were used between northern and southern California, including an offshore oil rig; the most frequented sites (in terms of number of sea lions) were Año Nuevo Island, Lighthouse Rock in Santa Cruz, and the Farallon Islands, with the remaining 15 sites used by one or at most two sea lions

(Fig. 2). An average of $49\% \pm 11\%$ of foraging trips started and ended at locations within 10 km of each other, which we interpreted as central place foraging given the three most frequented haul-out sites are >30 km apart.

The home range ($8,764 \text{ km}^2$) and core area ($1,873 \text{ km}^2$) of juvenile sea lions across the entire tracking duration was concentrated in central California between the Farallon Islands and Monterey Bay (Fig. 3). The exception to this was one sea lion that spent almost the entire tracking duration in a small area off northern California. The sizes of monthly core areas varied ($458\text{--}4,843 \text{ km}^2$), but were often focused on bathymetric regions in which turbulent mixing occurs. During November, the core area was concentrated just north of Santa Cruz, whereas there was an expanded range during December and January (Fig. 3). There was considerable individual variation in home range and core area sizes; some individuals restricted their movements to a relatively small area, repeatedly visiting the same areas trip after trip, while others appeared to range more widely (Table 2). All individuals generally foraged on the

Table 1. Animal and tag summary of satellite-tracked juvenile California sea lions, including sex, standard length (cm), estimated age range (yr), tracking duration (d), and tag type.

ID	Sex	Length (cm)	Estimated age (yr)	Duration (d)	Tag type
153501	M	125	2–3	171	SPOT 6
153502	F	122	1–2	243	SPOT 6
153504	F	123	1–2	154	SPOT 6
153505	F	135	2–3	191	SPOT 6
153506	M	141	2–3	127	SPLASH10F
153507	F	137	2–3	181	SPLASH10F

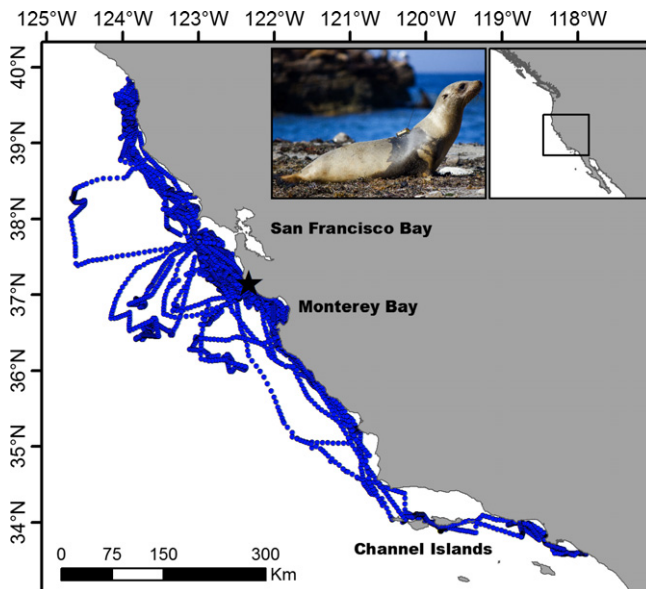


Figure 1. The at-sea locations of six juvenile California sea lions instrumented at Año Nuevo Island (denoted by the star). Photo by P. Robinson.

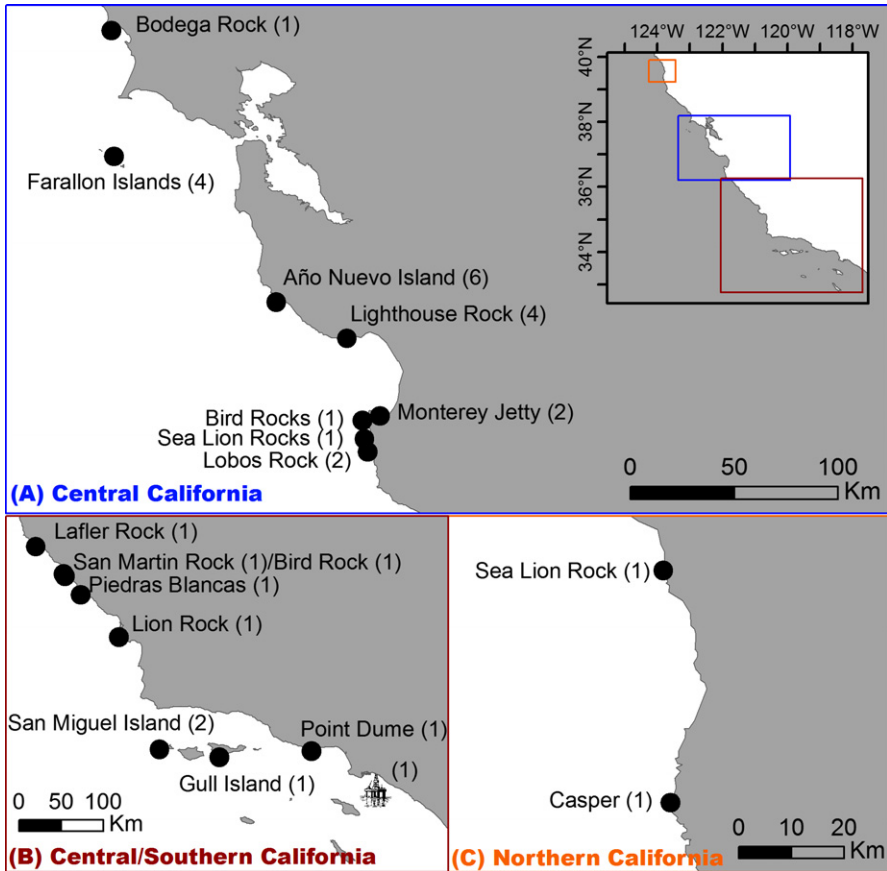


Figure 2. The haul-out locations that were used by six juvenile California sea lions instrumented at Año Nuevo Island. The number following the name of each location denotes the number of sea lions that used a particular haul-out.

continental shelf or near the 200 m isobath, but one sea lion had several foraging trips that were >100 km offshore (Table 2, Video S1).

We obtained data on over 9,000 individual dives for the two sea lions with dive tags (Fig. 4). The majority of dives were either U-shaped (47%–50%) or square-shaped (48%–49%), with very few V-shaped dives. The maximum dive depth and duration was achieved by the juvenile female at 363.5 m and 8.6 min, although these did not occur on the same dive. Overall, the juvenile male had greater mean dive depths (78.8 ± 73.8 m) and durations (2.5 ± 1.6 min) than the juvenile female (45.7 ± 39.2 m, 1.8 ± 1.0 min). Both sea lions had greater mean dive depths for U-shaped dives (110.4 and 55.5 m) compared with square-shaped dives (37.3 and 35.9 m), which tended to be very shallow and similar in depth between the two sea lions. The histogram data revealed similar trends (Fig. 4); the greatest proportion of dives were between 10 and 50 m and <2.5 min, but the juvenile male spent a considerable

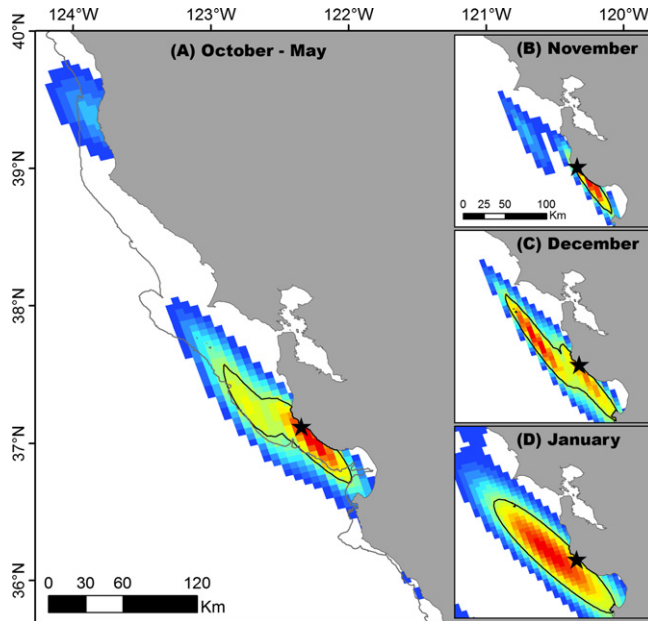


Figure 3. The home range (90% UD) and core area (50% UD) of six juvenile California sea lions instrumented at Año Nuevo Island (denoted by the star). The main plot shows the home range from the entire tracking duration (A, October–May), whereas each subplot (B–D) primarily shows the core area for the three months where tracking data existed for all six sea lions for the entire month (November, December, and January). The gray line depicts the 200 m isobath (A only) and the black line depicts the 50% UD (all plots). Colors indicate cells of high (warm colors) and low (cool colors) use.

amount of the tracking duration on long, deep dives (~20% of dives >100 m and 38% of dives >3 min).

Our findings indicate that juvenile California sea lions from Año Nuevo Island primarily use continental shelf habitat in close proximity to haul-out sites in central California waters, but will occasionally forage in offshore areas and waters of northern and southern California. Although we primarily tracked juveniles during the fall and winter months, we suspect this pattern likely persists during other times of the year, as shipboard surveys off the central California coast during the spring and early summer of 1996–2009 showed that sea lions were frequently sighted within the core areas we identified in our study (Santora *et al.* 2012). Juvenile sea lions instrumented at San Miguel Island in southern California generally exhibited similar patterns with respect to habitat use and proximity to coastal areas as those in our study, although during winter the majority of high use areas were confined to southern California waters (Orr 2011). The contrasting patterns in high use areas between juvenile sea lions in southern *vs.* central California indicates that there is likely partial spatial segregation of foraging areas among haul-out sites. This is not surprising because unlike lactating females, juveniles are not tied to a single haul-out location and can therefore use additional haul-out sites in close proximity to preferred foraging sites. This also explains why they often use a central-place foraging strategy. Although the birth rookery of instrumented sea lions in our study was unknown, it is unlikely that this

Table 2. Summary statistics of foraging trips (trips ≥ 6 h) and habitat use for juvenile California sea lions instrumented at Año Nuevo Island. Trip statistics include the number of trips, trip duration (d), haul-out duration (h), and time between trips (h), and time between trips (h). Habitat use statistics include the size of each sea lion's home range (90% UD) and core area (50% UD), the percentage of locations on the continental shelf, and the mean distance from the continental shelf and mainland coast. Values are presented as mean \pm SD (maximum) where applicable.

ID	# Trips	Duration (d)	Haul-out (h)	Between trips (h)	90% (km ²)	50% (km ²)	Continental shelf (%)	Continental shelf (km)	Mainland (km)
153501	91	1.2 \pm 1.2 (5.7)	3.6 \pm 6.5 (32)	14.6 \pm 25.4 (207)	1,345	292	87	6 \pm 6 (68)	13 \pm 12 (94)
153502	93	1.1 \pm 1.4 (8.9)	4.0 \pm 7.2 (41)	36.8 \pm 51.6 (277)	5,493	1,529	89	7 \pm 4 (56)	9 \pm 15 (65)
153504	87	1.2 \pm 1.3 (7.0)	2.7 \pm 4.2 (19)	13.5 \pm 17.2 (93)	5,540	872	92	10 \pm 7 (50)	15 \pm 13 (84)
153505	107	1.4 \pm 1.2 (4.9)	3.9 \pm 6.4 (35)	9.3 \pm 13.0 (105)	2,627	779	85	7 \pm 7 (66)	28 \pm 10 (79)
153506	64	1.3 \pm 1.3 (5.3)	7.1 \pm 10.2 (58)	16.8 \pm 16.6 (90)	1,724	475	91	8 \pm 5 (31)	7 \pm 6 (33)
153507	44	2.7 \pm 3.0 (12.4)	11.6 \pm 17.8 (104)	32.0 \pm 34.6 (184)	11,158	1,554	69	22 \pm 33 (134)	32 \pm 42 (164)

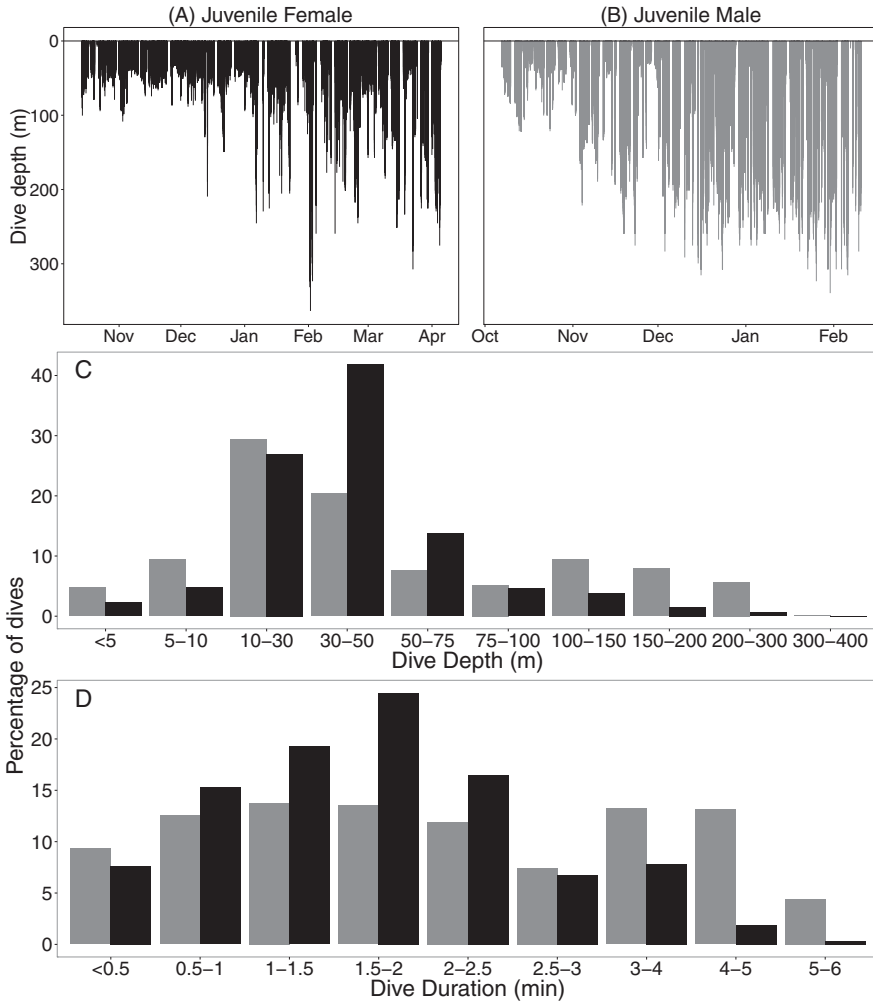


Figure 4. Dive behavior of two juvenile California sea lions instrumented at Año Nuevo Island. The top panel shows dive depth *vs.* time (A - B), and the bottom panel shows the percentage of dives at different ranges of dive depth (C) and duration (D) for each sea lion.

segregation was due to natal site fidelity given the small number of sea lions born at Año Nuevo Island (50–100 pups) compared with southern California rookeries (30,000+ pups; Lowry *et al.* 2017).

Adult California sea lions are typically characterized as shallow, epipelagic divers that primarily forage in continental shelf habitat (Weise *et al.* 2006, Melin *et al.* 2008, McHuron *et al.* 2016), and our study provides evidence that this generalization is likely true of juvenile sea lions as well. Despite the strong dependence on prey found within the epipelagic zone, diet and bio-logging data indicate adults and subadult males use multiple foraging strategies that also reflect dependence on benthic and mesopelagic prey (Weise *et al.* 2010, Orr *et al.* 2011, McHuron *et al.* 2016).

Our data indicate that these foraging strategies may develop at a relatively young age; both juveniles in our study exhibited a considerable number of presumably benthic dives (~50% of dives were square-shaped), and there was variation between the two sea lions with respect to dive depth, with one individual routinely diving to depths >100 m. The average dive depths and duration of the two juvenile sea lions were similar to adult dive behavior, but their maximum dive depths and durations were still only approximately 70% of adult maximum values (Weise *et al.* 2010, Kuhn and Costa 2014). This suggests that juveniles have a limited capability to exploit prey found at depths >300 m due to incomplete development of total oxygen stores and a smaller body size (Weise and Costa 2007), which is consistent with comparisons of juvenile and adult diving ability for other otariid species (Fowler *et al.* 2006, Jeglinski *et al.* 2012, Leung *et al.* 2014).

There are no behavioral data available for adult sea lions during the time period of our study for direct comparison, but data collected during other El Niño events or anomalous periods of increased SST suggest that juvenile and adult sea lions may differ in their response to environmental variation. For example, Weise *et al.* (2006) found that adult male sea lions from central California traveled farther offshore (up to 450 km) and had longer dive durations during the anomalously warm conditions of 2004–2005, whereas during 2003–2004 males foraged almost exclusively on the continental shelf. Similarly, adult female sea lions instrumented at San Miguel Island during the 1993 El Niño foraged exclusively in offshore habitat and had greater dive depths and durations than females during non El Niño conditions. There was one juvenile sea lion in our study that had several foraging trips that were >100 km offshore; however, she was one of the largest instrumented animals and all of the remaining animals primarily foraged over the continental shelf. Ontogenetic differences to environmental variation has been documented in a closely related species, the Galapagos sea lion (*Z. wolfebaeki*), where adult females dived deeper and longer during an El Niño event while juvenile behavior remained similar irrespective of oceanographic conditions (Jeglinski *et al.* 2012). It is possible that the apparent lack of a behavioral shift for sea lions in our study was because the 2015–2016 El Niño did not have the anticipated oceanographic effects on the central and southern California Current typically associated with such a strong El Niño index (Jacox *et al.* 2016). Although the abundance of forage fish typically consumed by sea lions was low during 2015 and 2016 (McClatchie *et al.* 2016b), camera tags placed on humpback whales (*Megaptera novaeangliae*) in central California during our study showed numerous sea lions feeding on anchovies (*Engraulis mordax*; BAB, personal observation). Alternative, albeit less-energy rich, prey sources may have also been available, as young-of-the-year rockfish (*Sebastes* spp.) were abundant off central California during this time period (McClatchie *et al.* 2016b) and in November market squid (*Doryteuthis opalescens*) were observed and taken in the commercial fishery within the core area of juvenile sea lions for that month (BAB, personal observation). Alternatively, it is possible that the apparent lack of a behavioral response by juvenile sea lions to the 2015–2016 El Niño event resulted from physiological limitations, as juveniles did not appear capable of reaching the maximum dive depths or durations of adult sea lions. As this is the first study to document the diving behavior of juvenile California sea lions and the first to track animals from this haul-out, we also cannot rule out that juveniles responded in a way that we were unable to detect, such as changes in dive effort, trip characteristics, or fine-scale habitat use.

Overall, these data suggest that foraging habitats in close proximity to haul-out sites are important for juvenile California sea lions, which appears to be a characteristic shared by several other juvenile otariids (Loughlin *et al.* 2003, Raum-Suryan *et al.* 2004, Fowler *et al.* 2006). There was temporal variation in the location and size of the home range and core areas, which was likely driven by the dynamic nature of oceanographic conditions in this area that affect the abundance and distribution of prey resources (Santora *et al.* 2012). Similar to the findings of Orr (2011), there were also differences in home range and core area locations and sizes among individuals, which may be related to individual differences in foraging behavior, such as prey type or foraging success. Juvenile California sea lions exhibited movement and diving patterns that were generally similar to but did not appear to reach the maximum capabilities of adults. The apparent spatial and vertical overlap between juvenile and adult sea lions may place them in direct competition, although this competitive pressure may be alleviated during periods of reduced prey availability because adults have greater flexibility than juveniles to exploit additional habitats to meet their energy requirements. The physiological limitations associated with a small body size and incomplete development of oxygen stores likely restricts juveniles to foraging on or just off the continental shelf, limiting their behavioral responses during periods of reduced prey availability largely to north-south movements and subtler changes in dive behavior and dive effort. Given the limited scope and small sample size of our study, concurrent tracking of adult and juvenile California sea lions and more extensive data on the diving behavior of juveniles are necessary to provide additional support for these conclusions.

ACKNOWLEDGMENTS

Sea lions were handled under NMFS Permits #17115 and 17952 and IACUC approval from the University of California Santa Cruz. We would like to thank Jamie Lloyd-Smith, Katie Prager, Denise Greig, Patrick Robinson, the Marine Mammal Center, the volunteers that assisted with the field effort, and the Año Nuevo State Park rangers for making this project possible. This project was supported by funding from the National Science Foundation (OCE - 1335657) to J. Lloyd-Smith and K. Prager, and from Discovery Communications and True Blue Films to BAB.

LITERATURE CITED

- Baylis, A. M. M., R. A. Orben, D. P. Costa, M. Tierney, P. Brickle and I. J. Staniland. 2017. Habitat use and spatial fidelity of male South American sea lions during the nonbreeding period. *Ecology and Evolution* 7:3992–4002.
- Börger, L., N. Franconi, G. De Michele, *et al.* 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75:1393–1405.
- Carretta, J. V., E. M. Oleson, D. W. Weller, *et al.* 2015. U.S. Pacific marine mammal stock assessments: 2014. U.S. Department of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-549. 414 pp.
- Costa, D. P., P. W. Robinson, J. P. Y. Arnould, *et al.* 2010. Accuracy of ARGOS locations of pinnipeds at-sea estimated using Fastloc GPS. *PLOS ONE* 5:e8677.
- Fowler, S. L., D. P. Costa, J. P. Y. Arnould, N. J. Gales and C. E. Kuhn. 2006. Ontogeny of diving behavior in the Australian sea lion: Trials of adolescence in a late bloomer. *Journal of Animal Ecology* 75:358–367.

- Gales, N. J., and R. J. Mattlin. 1998. Fast, safe, field-portable gas anesthesia for otariids. *Marine Mammal Science* 14:355–361.
- Hazen, E. L., S. M. Maxwell, H. Bailey, *et al.* 2012. Ontogeny in marine tagging and tracking science: Technologies and data gaps. *Marine Ecology Progress Series* 457:221–240.
- Horning, M., and F. Trillmich. 1997. Ontogeny of diving behavior in the Galapagos fur seal. *Behaviour* 134:1211–1257.
- Hückstädt, L. A., R. A. Quiñones, M. Sepúlveda and D. P. Costa. 2014. Movement and diving patterns of juvenile male South American sea lions off the coast of central Chile. *Marine Mammal Science* 30:1175–1183.
- Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore and S. J. Bograd. 2016. Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophysical Research Letters* 43:7072–7080.
- Jeglinski, J. W. E., C. Werner, P. W. Robinson, D. P. Costa and F. Trillmich. 2012. Age, body mass and environmental variation shape the foraging ontogeny of Galapagos sea lions. *Marine Ecology Progress Series* 453:279–296.
- Jeglinski, J. W. E., K. T. Goetz, C. Werner, D. P. Costa and F. Trillmich. 2013. Same size – same niche? Foraging niche separation between sympatric juvenile Galapagos sea lions and adult Galapagos fur seals. *Journal of Animal Ecology* 82:694–706.
- Johnson, D., J. London, M. Lea and J. Durban. 2008. Continuous-time correlated random walk model for animal telemetry data. *Ecology* 89:1208–1215.
- Koslow, J. A., P. Davison, A. Lara-Lopez and M. D. Ohman. 2014. Epipelagic and mesopelagic fishes in the southern California Current System: Ecological interactions and oceanographic influences on their abundance. *Journal of Marine Systems* 138:20–28.
- Kuhn, C. E., and D. P. Costa. 2014. Interannual variation in the at-sea behavior of California sea lions (*Zalophus californianus*). *Marine Mammal Science* 30:1297–1319.
- Laake, J. L., S. R. Melin, A. J. Orr, D. J. Greig, K. C. Prager, R. L. DeLong and J. D. Harris. 2016. California sea lion sex- and age-specific morphometry. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-312. 21 pp.
- Leung, E. S., B. L. Chilvers, S. Nakagawa and B. C. Robertson. 2014. Size and experience matter: Diving behavior of juvenile New Zealand sea lions (*Phocarctos hookeri*). *Polar Biology* 37:15–26.
- Loughlin, T. R., J. T. Sterling, R. L. Merrick, J. L. Sease and A. E. York. 2003. Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). *Fisheries Bulletin* 101:566–582.
- Lowry, M. S., S. R. Melin and J. L. Laake. 2017. Breeding season distribution and population growth of California sea lions, *Zalophus californianus*, in the United States during 1964–2014. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-SWFSC-574. 63 pp.
- McClatchie, S., J. Field, A. R. Thompson, *et al.* 2016a. Food limitation of sea lion pups and the decline of forage off central and southern California. *Royal Society Open Science* 3:150628.
- McClatchie, S., R. Goericke, A. Leising, *et al.* 2016b. State of the California Current 2015–16: Comparisons with the 1997–98 El Niño. *California Cooperative Oceanic Fisheries Investigations Report* 57:5–61.
- McHuron, E. A., P. W. Robinson, S. E. Simmons, C. E. Kuhn, M. Fowler and D. P. Costa. 2016. Foraging strategies of a generalist marine predator inhabiting a dynamic environment. *Oecologia* 182:995–1005.
- Melin, S. R., R. DeLong and D. Siniff. 2008. The effects of El Niño on the foraging behavior of lactating California sea lions (*Zalophus californianus californianus*) during the nonbreeding season. *Canadian Journal of Zoology* 86:192–206.
- Melin, S. R., A. Orr, J. D. Harris and R. DeLong. 2012. California sea lions: An indicator for integrated ecosystem assessment of the California Current System. *California Cooperative Oceanic Fisheries Investigations Report* 53:140–152.

- Ono, K. A., D. J. Boness and O. T. Oftedal. 1987. The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. *Behavioral Ecology and Sociobiology* 21:109–118.
- Orr, A. J. 2011. Foraging ecology of immature California sea lions (*Zalophus californianus*). Ph.D. dissertation, University of Washington, Seattle, WA. 206 pp.
- Orr, A. J., G. VanBlaricom, R. L. DeLong, V. H. Cruz-Escalano and S. D. Newsome. 2011. Intraspecific comparison of diet of California sea lions (*Zalophus californianus*) assessed using fecal and stable isotope analyses. *Canadian Journal of Zoology* 89:109–122.
- Orr, A. J., S. D. Newsome, J. L. Laake, G. R. VanBlaricom and R. L. DeLong. 2012. Ontogenetic dietary information of the California sea lion (*Zalophus californianus*) assessed using stable isotope analysis. *Marine Mammal Science* 28:714–732.
- Ralston, S., J. C. Field and K. M. Sakuma. 2015. Long-term variation in a central California pelagic forage assemblage. *Journal of Marine Systems* 146:26–37.
- Raum-Suryan, K. L., M. J. Rehberg, G. W. Pendleton, K. W. Pitcher and T. S. Gelatt. 2004. Development of dispersal, movement patterns, and haul-out use by pup and juvenile Steller sea lions (*Eumetopias jubatus*) in Alaska. *Marine Mammal Science* 20:823–850.
- Santora, J. A., J. C. Field, I. D. Schroeder, K. M. Sakuma, B. K. Wells and W. J. Sydeman. 2012. Spatial ecology of krill, micronekton and top predators in the central California Current: Implications for defining ecologically important areas. *Progress in Oceanography* 106:154–174.
- Trillmich, F., and D. Limberger. 1985. Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia* 67:19–22.
- Trillmich, F., K. A. Ono, D. P. Costa, *et al.* 1991. The effects of El Niño on pinniped populations in the Eastern Pacific. Pages 247–270 *in* F. Trillmich and K. A. Ono, eds. *Pinnipeds and El Niño*. Springer-Verlag, Berlin, Germany.
- Weise, M. J., and D. P. Costa. 2007. Total body oxygen stores and physiological diving capacity of California sea lions as a function of sex and age. *Journal of Experimental Biology* 210:278–289.
- Weise, M. J., and J. T. Harvey. 2008. Temporal variability in ocean climate and California sea lion diet and biomass consumption: Implications for fisheries management. *Marine Ecology Progress Series* 373:157–172.
- Weise, M. J., D. P. Costa and R. M. Kudela. 2006. Movement and diving behavior of male California sea lion (*Zalophus californianus*) during anomalous oceanographic conditions of 2005 compared to those of 2004. *Geophysical Research Letters* 33:L22S10.
- Weise, M. J., J. T. Harvey and D. P. Costa. 2010. The role of body size in individual-based foraging strategies of a top marine predator. *Ecology* 91:1004–1015.
- Zaba, K. D., and D. L. Rudnick. 2016. The 2014–2015 warming anomaly in the Southern California Current System observed by underwater gliders. *Geophysical Research Letters* 43:1241–1248.

Received: 9 March 2017

Accepted: 2 August 2017

SUPPORTING INFORMATION

The following supporting information is available for this article online at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12449/supinfo>.

Video S1. Video animation of tracking data collected from juvenile California sea lions instrumented at Año Nuevo Island, highlighting their use of continental shelf habitat.