UNPRECEDENTED MORTALITY OF CALIFORNIA SEA LION PUPS ASSOCIATED WITH ANOMALOUS OCEANOGRAPHIC CONDITIONS ALONG THE CENTRAL CALIFORNIA COAST IN 2009

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ABSTRACT

Between May and August 2009, an anomalous oceanographic event occurred along the central California coast. The event was characterized by the strongest negative upwelling observed in 40 years and uncharacteristically warm sea surface temperatures. The timing of the event coincided with the weaning and reproduction of California sea lions in the California Current System. We documented the effects of the event on sea lion pup production, pup mortality, female attendance, and diet at San Miguel Island, California. Simultaneous with the oceanographic event, we also documented a record number of strandings along the California coast of emaciated weaned pups born in 2008. We conclude that the response of California sea lions to the anomalous oceanographic conditions in 2009 was mediated through warmer SSTs that likely reduced availability of their usual summer prey and resulted in the high mortality of the 2008 and 2009 cohorts due to starvation.

INTRODUCTION

The California sea lion (*Zalophus californianus*) population has been growing steadily since its protection under the Marine Mammal Protection Act of 1972 (Caretta et al. 2007). During its period of rapid growth in the 1970s and 1980s, the population experienced significant declines in production during 1982–1983, 1992–1993 and 1998 that were associated with El Niño (EN) events (DeLong et al. 1991; DeLong and Melin 2000; Caretta et al. 2007). The response of California sea lions to EN conditions is presumably mediated through a change in the availability of fish and cephalopods, the primary prey of California sea lions (DeLong et al. 1991; DeLong and Melin 2000). In the California Current System (CCS), EN conditions are characterized by a change in sea level pressure that leads to increased coastal sea level height (Norton et al. 1985), delayed onset of the upwelling season (Bograd et al. 2009), a decrease in the upwelling strength, increased sea surface temperature (SST), and suppression of the thermocline (Norton et al. 1985). These changes result in lower productivity at lower trophic levels which results in reduced availability of fish and cephalopods at upper trophic levels (Barber and Chavez 1983; Chavez et al. 2002). However, anomalous oceanographic conditions also occur outside EN and can have similar effects on the marine community structure at local or regional scales (Schwing et al. 2006). In 2005, a delayed onset of the seasonal upwelling in the northern CCS resulted from a regional shift in oceanographic dynamics (Schwing et al. 2006) and declines in productivity at various trophic levels were reported (Brodeur et al. 2006; Mackas et al. 2006; Sydeman et al. 2006; Thomas and Brickley 2006).

In 2009, and EN in the tropics was confirmed in July (http://www.noaanews.noaa.gov/stories2009/20090709_elnino.html). But, a regional anomalous oceanographic event began two months earlier in the south and central CCS. After a normal start to the upwelling season with strong positive upwelling conditions from February through April in the CCS, a shift to negative upwelling occurred in May (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html). The negative upwelling intensified in June and became the strongest negative upwelling event in the past 40 years. SSTs along the central coast were uncharacteristically warm as a result of the reduced upwelling. By September, positive upwelling conditions and cooler SSTs had returned to the CCS. The timing of the event was simultaneous with the weaning and reproductive seasons for California sea lions breeding in the southern CCS. Here, we document the unprecedented mortality of pups born at San Miguel Island, California, and a record number of strandings of emaciated, weaned pups from the 2008 cohort along the central California coast that occurred during the event.

California Sea Lion Life History

California sea lions are permanent residents of the CCS, ranging from northern Mexico to southern Canada. In the United States, the primary breeding colonies are the California Channel Islands. Weaning

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and reproduction occur during late spring and summer, during the peak upwelling period in the CCS (Bograd et al. 2009). During the reproductive season, adult females give birth to a single pup during a 6-week period from late May to the end of June (Peterson and Bartholomew 1967). Lactation lasts up to 11 months or longer. During this time, lactating females travel to sea for 2–5 days to feed and return to the colony for 2 days to nurse their pup (Antonelis et al. 1990; Melin et al. 2000). The pup is solely dependent on its mother until about 6 months old and maintains a fasting cycle while the mother is on foraging trips. The weaning process is gradual and the timing of weaning is poorly known but it begins as early as 8 months old. Peak weaning occurs in April or May when pups are between 10 and 11 months old (Melin et al. 2000).

Adult females and pups from San Miguel Island generally remain south of Monterey Bay, California year-round and feed in coastal waters in the summer and move offshore in the winter (Melin and DeLong 2000; Melin et al. 2008). California sea lions in the Channel Islands feed on more than 30 fish and cephalopod species (Antonelis et al. 1984; Lowry et al. 1990; Antonelis et al. 1990; Lowry 1991) and generally feed within 75 m of the surface but have been reported to dive deeper than 480 m (Feldkamp et al. 1989; Melin et al. 2008).

Oceanographic Indices

The most dominant feature of the CCS is the seasonal upwelling that occurs between January and November each year (Lynn and Simpson 1987; Bograd et al. 2009). Off the central California coast (Point Conception to Cape Mendocino), peak upwelling and productivity usually occurs between April and July when California sea lion pups born the previous year are weaned and a new cohort is born.

During periods of strong negative upwelling in the CCS, such as during ENSO events, regional productivity declines and lactating female California sea lions travel farther from the colony, move farther offshore and dive deeper presumably in response to movement of their prey deeper in the water column or to more productive areas (Melin et al. 2008). Because lactating females are restricted in the distance they can travel and the time they are away from the colony by the fasting capabilities of their pups, movement of their prey outside their normal foraging range (spatially or temporally) results in longer foraging trips (Melin et al. 2000; Melin et al. 2008). This can have negative consequences for a dependent pup. If the duration of the foraging trip exceeds the fasting capability of the pup, the pup may die from starvation and if the female is unable to obtain enough prey or energy for self-maintenance and lacta-

tion, she may not be able to support her pup. For newly weaned pups, the movement of prey out of their foraging range or to deeper depths may result in starvation (Fowler et al. 2007). Thus, indices of upwelling strength and SST may provide proxies for prey availability and explain events like the unusually high pup mortality at San Miguel Island and high incidence of stranded yearlings observed along the central California coast in 2009. Here, we use oceanographic indices to explain annual patterns in pup production and mortality indices of the California sea lion population at San Miguel Island, California, and strandings of weaned pups along the central California coast between 1997 and 2009.

METHODS

California Sea Lion Population Indices

Study Sites We measured several population indices for the California sea lion population at San Miguel Island, California (34.03°N, 120.4°W). San Miguel Island represents the northern extent of the breeding range and is one of the largest colonies in the Channel Islands representing about 45% of the U. S. breeding population. As such, it is a useful colony to measure trends and population responses to changes in the marine environment. Because of the large size of the colony, we used index sites for measuring the population parameters. The East Adams Cove Study Area (EACS) is a long-term index site for measuring the timing of reproductive events of a small group of animals (~800 females). West Shelf Rock (WSR) is a small rocky cove where individually marked animals are easily observed and was used as the site for monitoring attendance cycles of females in 2009. The Point Bennett Study Area (PBSA) is used as a long-term index site for monitoring pup production and mortality. About 50% of the pup production that occurs at San Miguel Island takes place in this area, so it provides an index of trends for the entire colony.

Median Birthing Date Between 15 May and 20 July each year between 1997 and 2009, the total numbers of live and dead sea lion pups in the EACS were counted daily to obtain a cumulative count of pups born over the reproductive season. The median birth date was calculated as the date by which 50% of the pups were born. The temporal trend in births was described from the weekly maximum number of pups counted in the EACS. The long-term means for median birth date and maximum number of pups were calculated for 1997–2008, excluding 1998. We excluded 1998 from the long-term dataset because it was an ENSO year and the temporal pattern of births and median birth date were abnormal.

Female Attendance Cycle We conducted 12-hour daily observations of seven branded females at WSR

between 19 June and 21 July 2009. Once a female gave birth, we monitored her attendance. If a female was observed at any time during the observation period, she was considered present for the full day. The small size of the cove and the intensive observation time each day made it unlikely that a female that was present would not be observed. The first foraging trip (post-natal trip) was shorter than subsequent trips for all females (Student's paired T-test, $p = 0.03$), so we calculated a mean for the first trip and a mean for all subsequent trips. A nested analysis of variance (ANOVA) with foraging trips nested within individual females was used to calculate the overall mean for the foraging trips that occurred after the post-natal trips. We compared the attendance pattern in 2009 with previous studies at San Miguel Island in the 1980s (Feldkamp et al. 1989; Antonelis et al. 1990).

Pup Mortality   Pup mortality surveys were conducted every 2 weeks from 25 June to early August between 1997 and 2009 in the PBSA as an index of pup mortality for the population. A final survey was conducted the last week of September. Dead pups were removed from the breeding areas as they were counted so they would not be recounted on subsequent surveys. The total number of observed dead pups for each survey described the temporal trend in pup mortality and was an estimate of the cumulative mortality of pups at 5 weeks and 3.5 months of age.

Pup Production   Live pups were counted in the PBSA after all pups were born (between 20–30 July) each year between 1997 and 2009. Observers walked through the PBSA, moved adults away from pups, and then counted individual pups. A mean number of live pups for the PBSA was calculated from the total number of live pups counted by each observer. Total production was the sum of the mean number of live pups and the cumulative number of dead pups counted up to the time of the live pup survey. Cumulative pup mortality at 5 weeks of age was calculated as the proportion of dead pups of those counted during the live pup survey. This mortality rate was used to model pup mortality trends over time.

Strandings of California Sea Lion Pups   We compiled stranding data for animals that live stranded from San Luis Obispo to Mendocino counties in central California and that were transported to The Marine Mammal Center (TMMC) in Sausalito, California, for rehabilitation to describe trends in strandings of weaned pups between 1997 and 2009. We restricted the stranding dataset to those recovered by TMMC because they are responsible for strandings that occur over the largest area of the central coast and have had consistent recovery effort from 1997 to 2009. The stranding data represent the minimum number of animals that stranded

in any year because strandings that occurred in remote areas are not reported and animals that died prior to collection were not included. We excluded dead animals because the cause of death could not be determined. We restricted the dataset to pups of the year that were evaluated by veterinarians at the TMMC to have stranded due to starvation. Pups were classified as animals that were between 0- and 1-year-old with a birth date of 15 June.

Diet Composition and Prey Identification   We collected fecal samples from adult female California sea lion haul out areas at San Miguel Island in July or early August in the early 2000s (2000, 2001, 2002, 2004, 2005) and 2009 to examine the diet. Individual samples were placed in bags and frozen until they were processed for prey identification. Fecal samples contained in nylon paint strainer bags were washed in a washing machine to remove fecal matter and the remaining contents were washed through nested sieves to recover fish bones, fish otoliths and cephalopod hard parts that were then identified to family, genus or species (Orr et al. 2003). The similarity of key otolith structures and the degradation from digestion of *Sebastes* spp. otoliths made species identification difficult and we used the genus rather than risk misidentification of the species. Using all identifiable structures, the frequency of occurrence (FO) of each fish taxon was calculated as the number of samples containing the taxon of the total samples with identifiable prey remains. We used FO as a conservative relative measure of prey importance because of the biases associated with extrapolating from fecal contents to biomass or percent mass of prey consumed by pinnipeds (Laake et al. 2002; Joy et al. 2006). The primary fish taxons were defined as those that had FO greater than 10% in any year.

We calculated the diet composition as the percentage of samples that contained fish only, mixed fish and cephalopod, or cephalopod remains only. For each diet component and each fish taxon, a general linear model was constructed to test differences between 2009 and the other years.

Oceanographic Indices

Upwelling Index Anomaly   We used a monthly coastal upwelling index (UWI) anomaly between 1997 and 2009 as an index of monthly productivity and prey availability (Schwing et al. 2006). The upwelling index anomaly dataset was obtained from NOAA's Pacific Fisheries Environmental Laboratory (http://pfel. noaa.gov). We used the 33°N 119°W and 36°N 122°W indices because they encompassed the foraging range of juvenile and lactating female California sea lions (fig. 1). The baseline index was calculated from monthly means of upwelling between 1946 and 1986. The
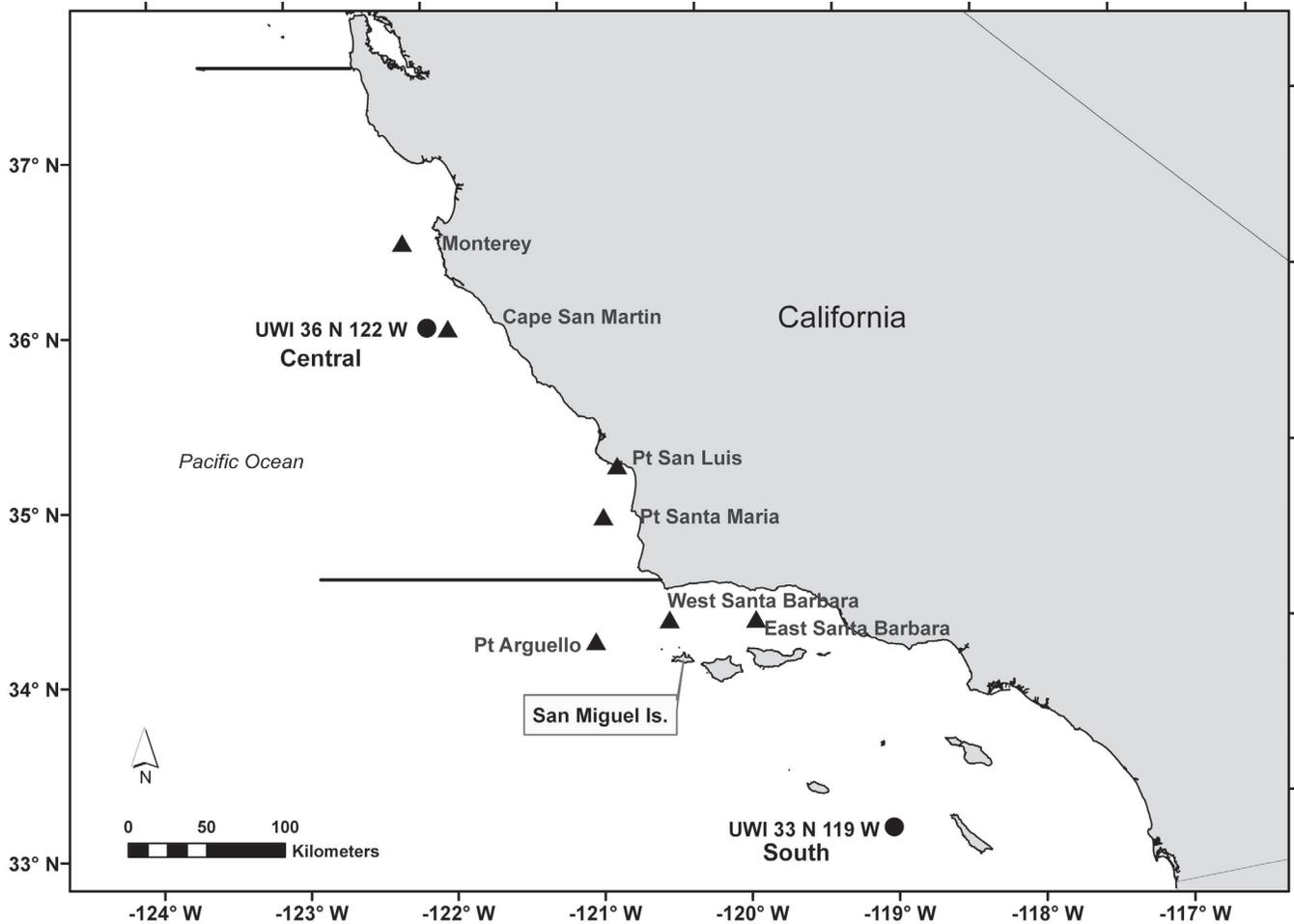
Figure 1.   Positions of buoys used to calculate the monthly sea surface temperature index (SSTI) anomaly (▲) and center positions of the monthly upwelling index (UWI) anomaly (●) based on 3° grids. South and central regions for the UWI are defined by horizontal lines.

monthly upwelling anomalies within each year are the difference between the baseline mean and the annual monthly mean.

Sea Surface Temperature Anomaly   We used SST anomalies as an indicator of prey availability. We calculated a daily mean SST from seven buoys along the central California coast (fig. 1). The buoy data were obtained from the NOAA National Data Buoy Center (http://www.ndbc.noaa.gov/rmd.shtml). We used the mean daily SST to calculate a mean monthly SST for each buoy and then created a monthly baseline SST for each buoy for the periods 1994 to 1996 and 1998 to 2008. Data for 1997 were not available for many of the months at several buoys, so it was excluded from the baseline calculation. For each buoy, the baseline monthly SST was subtracted from the mean SST value for each month in each year from 1997 to 2009 to construct a time series of anomalies. The anomalies were averaged

across the buoys for each month to create a sea surface temperature anomaly index (SSTI).

Model of Early Pup Mortality and Oceanographic Indices

We used R (R Core Development Team 2009) to develop linear models that included year, SSTI and UWI indices to explain the variability in pup mortality at 5 weeks of age between 1997 and 2009. We created four temporal variables for SSTI and UWI to reflect lags in the response of sea lions to oceanographic changes. The variables were as follows: April to July, May to July, May to June, and June to July. We also created a June only and July only variable to account for an immediate impact of oceanographic changes on pup mortality. For the UWI, we created separate variables for 33°N 119°W and 36°N 122°W for each temporal variable. We used the Akaike Information Criterion
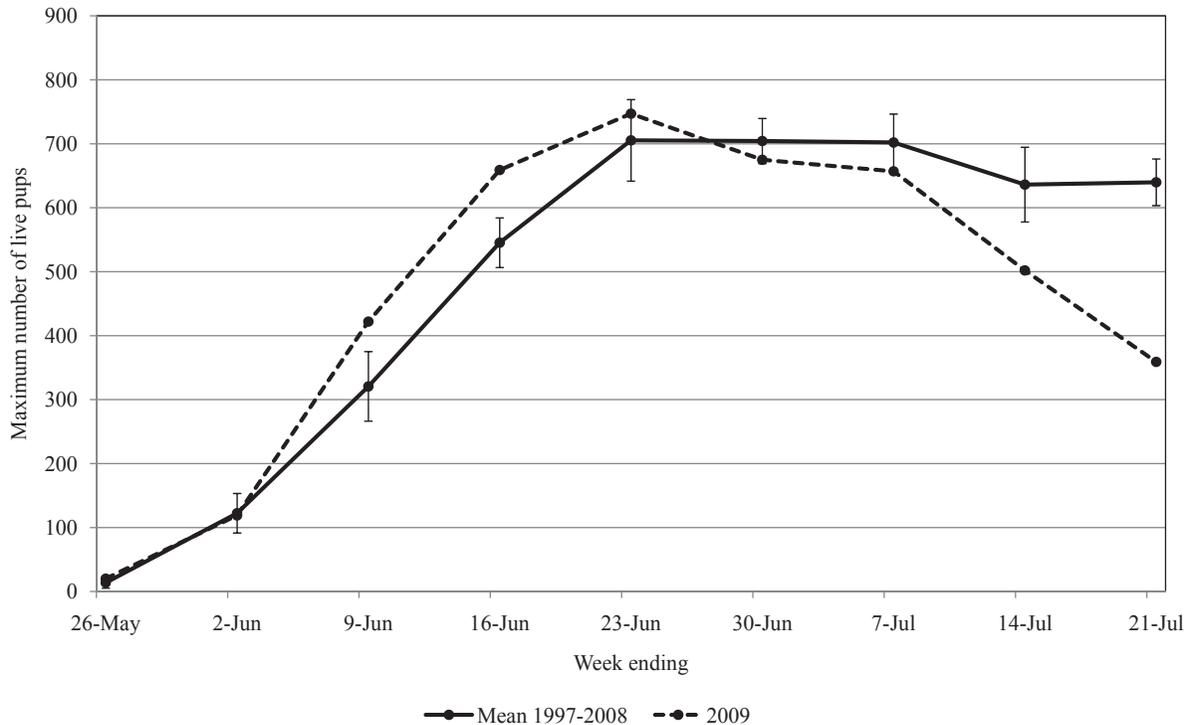
Figure 2. The weekly mean of the maximum number of live California sea lion pups counted in the East Adams Cove Study Area (EACS) at San Miguel Island, California, for 1997 to 2008 and the weekly maximum number of live pups counted in 2009. Error bars represent one standard error about the mean.

adjusted for small sample sizes (AICc) to select the best model (Burnham and Anderson 2002).

RESULTS

California Sea Lion Population Indices

Median Birthing Date   Births in the EACS in 2009 followed the long-term pattern with females giving birth beginning in late May, a median birth date of 9 June (1997–2008: mean = 10 June, SE = 0.982 days), the maximum number of live pups occurring by 23 June, and birthing completed by 30 June (fig. 2). The decline in the number of live pups after 7 July in 2009 reflects the high early pup mortality that occurred in late June and early July.

Female Attendance Cycle   Seven lactating females made between two and six foraging trips between 19 June and 21 July 2009. The mean post-natal foraging trip duration was 4.3 days (SE = 0.57 days). The mean of all subsequent trips was 7 days (SE = 1.89 days). The mean duration of the visits ashore was not different between the first visit after the post-natal foraging trip and subsequent visits (Student's paired T-test, $p = 0.57$) so the data were pooled. The mean visit ashore for the seven females was 1.9 days (SE = 0.82 days). Previous studies reported mean foraging trip durations of 3.1 days ($n = 25$ females, SE = 0.17 days; Antonelis et al. 1990) and 2.5 days ($n = 8$ females, SE = 0.49

days; Feldkamp et al. 1989) and visits ashore of 2.1 days (SE = 0.16 days; Antonelis et al. 1990).

Pup Production and Mortality   The estimated 2009 pup production for the PBSA was 14651 pups. This was similar to the long-term mean between 1997 and 2008 of 14521 (SE = 695 pups) (fig. 3). But early pup mortality during the first 5 weeks of life was 74% in 2009, almost four times greater than the long-term average of 18.7% (SE = 1.6%) (fig. 3).

Pup mortality to 3.5 months of age in 2009 had a dramatically different temporal pattern and magnitude from the long-term average (fig. 4). Pup mortality normally declines slowly from birth, reaching 15% by 1 month of age (fig. 4). The mortality accelerates between 2 and 3 months of age, culminating in a pup mortality rate of about 33% at 3.5 months of age. In 2009, most of the pup mortality occurred early in the season with 65% of the mortality occurring by 1 month of age (fig. 4). By 3.5 months of age, 80% of the pups born in 2009 had died.

Strandings of California sea lion pups   Strandings of emaciated pups from the 2008 cohort occurred in record numbers between San Luis Obispo and Mendocino counties in central California in 2009. The long-term mean from the 1997–2008 cohorts was 70 pups per year (SE = 24.0) but in 2009, 640 pups were recovered (fig. 5). Most of the strandings in 2009 occurred between May and August (92%) (fig. 6). Within this
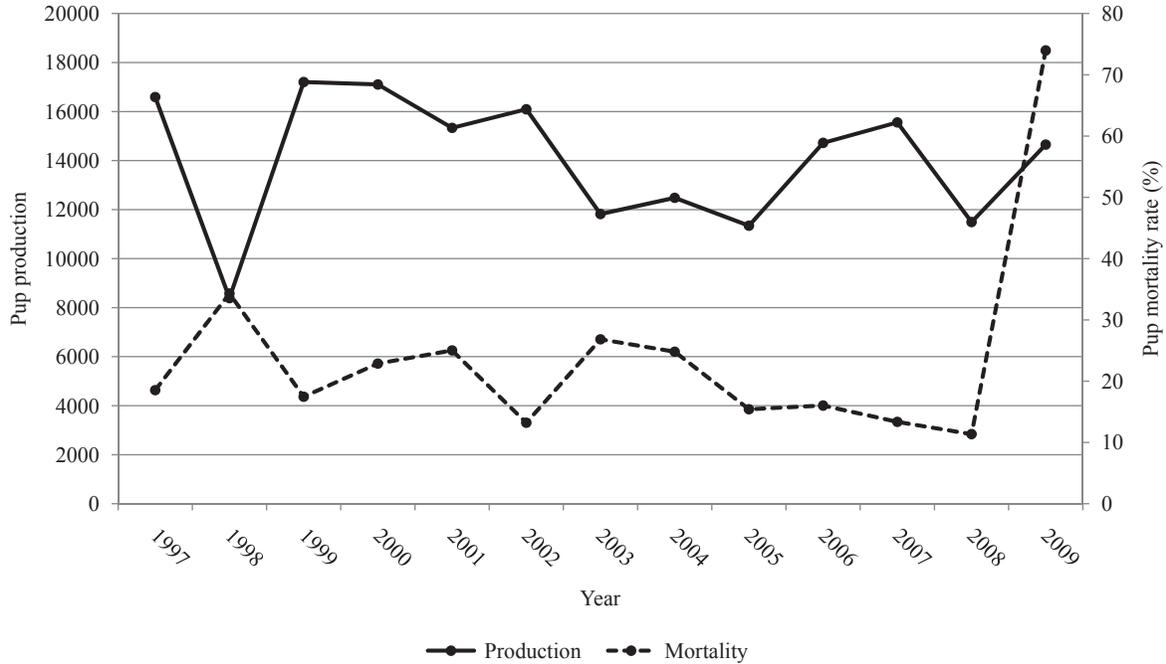
Figure 3.   The pup mortality rate at 5 weeks of age and the annual pup production of California sea lions in the Point Bennett Study Area (PBSA) on San Miguel Island, California, between 1997 and 2009.
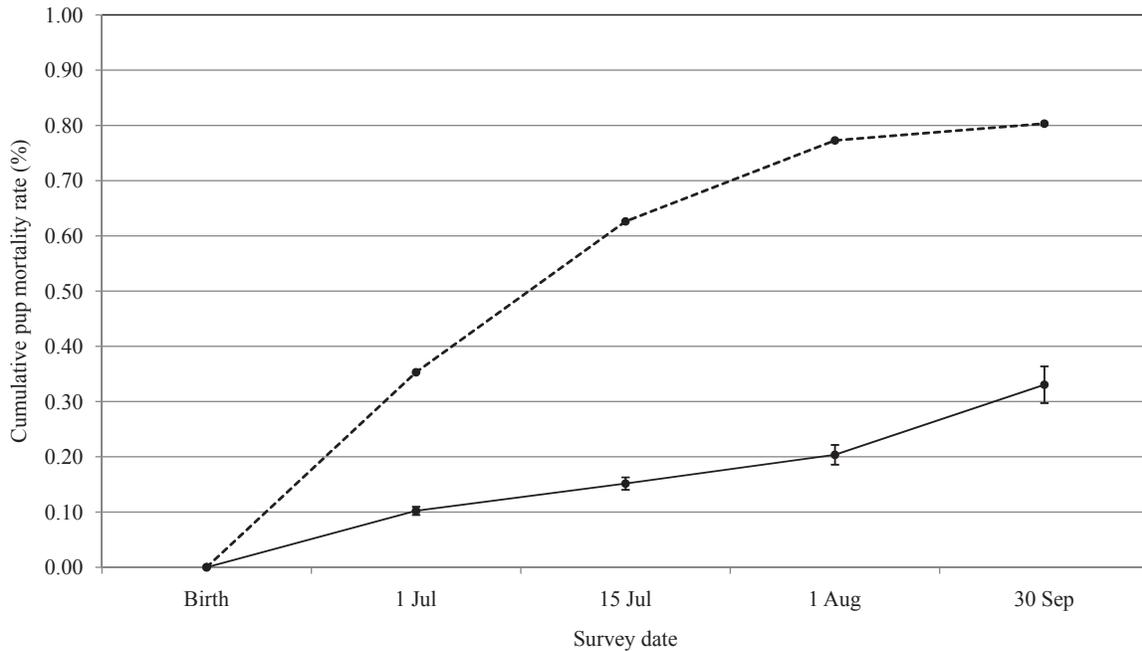
Figure 4.   The mean cumulative pup mortality rate for California sea lion pups in the Point Bennett Study Area (PBSA) on San Miguel Island, California, between 1997 and 2008 and for 2009 from birth to 3.5 months of age. Error bars represent one standard error about the mean.

period, most of the strandings occurred in June corresponding to the period of the warmest SSTI and most negative UWI anomalies (figs. 7 and 8).

Diet Composition and Prey Identification   We identified 36 fish taxons consumed by California sea lions including two new species not previously reported in the diet (tab. 1). Pacific hake, northern anchovy, Pacific sardine, rockfish, Pacific saury and jack mackerel comprised the primary fish prey. In the early 2000s, hake, anchovy and sardine dominated the fish diet, but in 2009 rockfish was the most frequent fish prey.

Fish and cephalopods comprised the diet of California sea lions during the summer and the frequency of the different components and primary fish prey varied
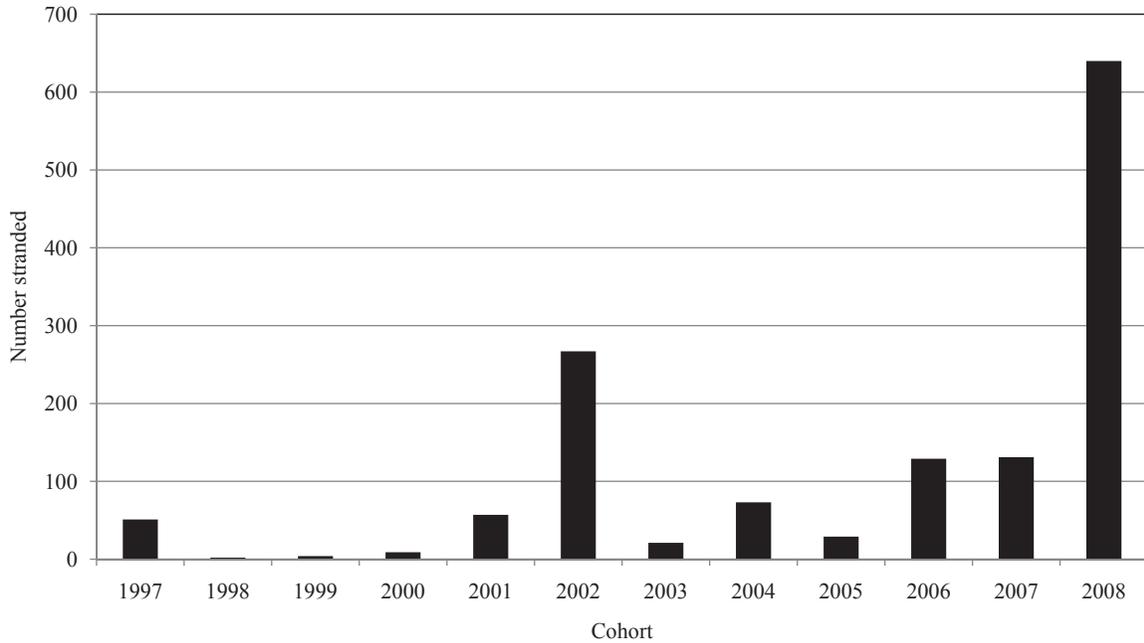
Figure 5.   The annual number of weaned California sea lion pups by cohort that stranded due to emaciation between San Luis Obispo and Mendocino counties along the central California coast and that were evaluated by The Marine Mammal Center in Sausalito, California, between 1997 and 2009.
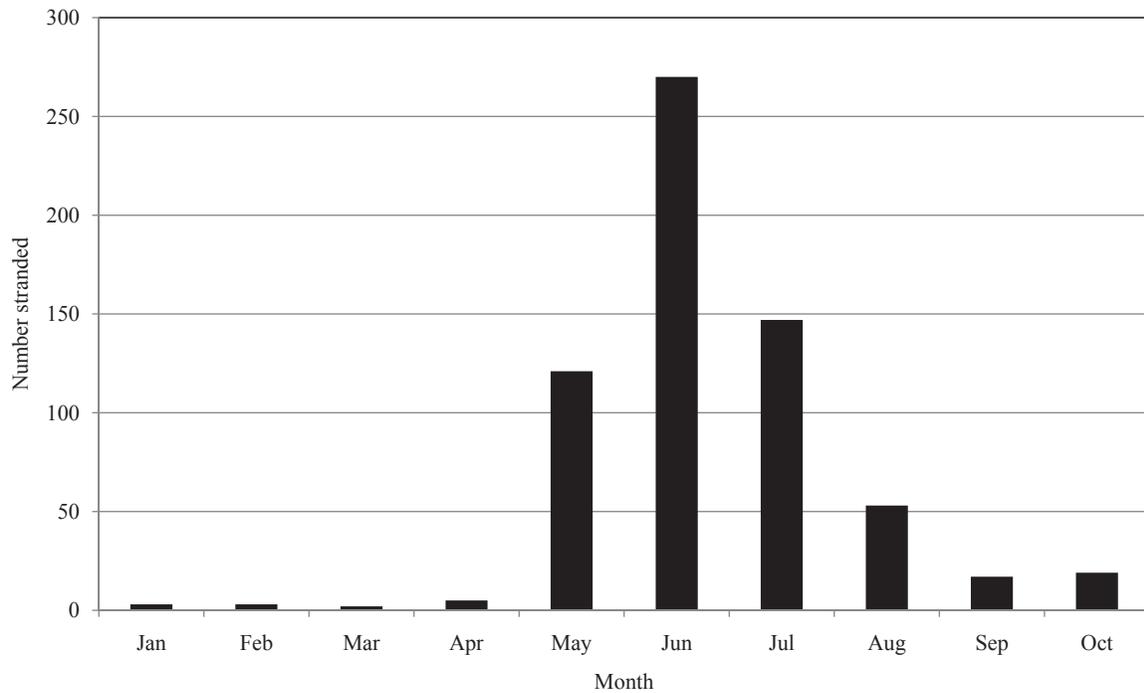
Figure 6.   The monthly distribution of weaned California sea lion pups from the 2008 cohort that stranded due to emaciation between San Luis Obispo and Mendocino counties along the central California coast and that were evaluated by The Marine Mammal Center in Sausalito, California, in 2009.

significantly from 2009 for many of the years (tab. 2). In 2009, the diet was comprised of 30.7% fish, 30.8% cephalopod and 38.5% mixed fish and cephalopods (tab. 3). The percentage of cephalopod only in the diet was significantly higher in 2009 (ANOVA, $p = 0.034$). Rockfish was the only primary prey that was significantly different in 2009, occurring more fre-

quently than in the early 2000s (ANOVA, $p = 0.028$) (tab. 3). The FO of northern anchovy, Pacific sardine, Pacific hake and Pacific saury were lower in 2009 than in the early 2000s but were not different for the two periods due to substantial annual variability in the frequencies of occurrence among the years (tab. 3).
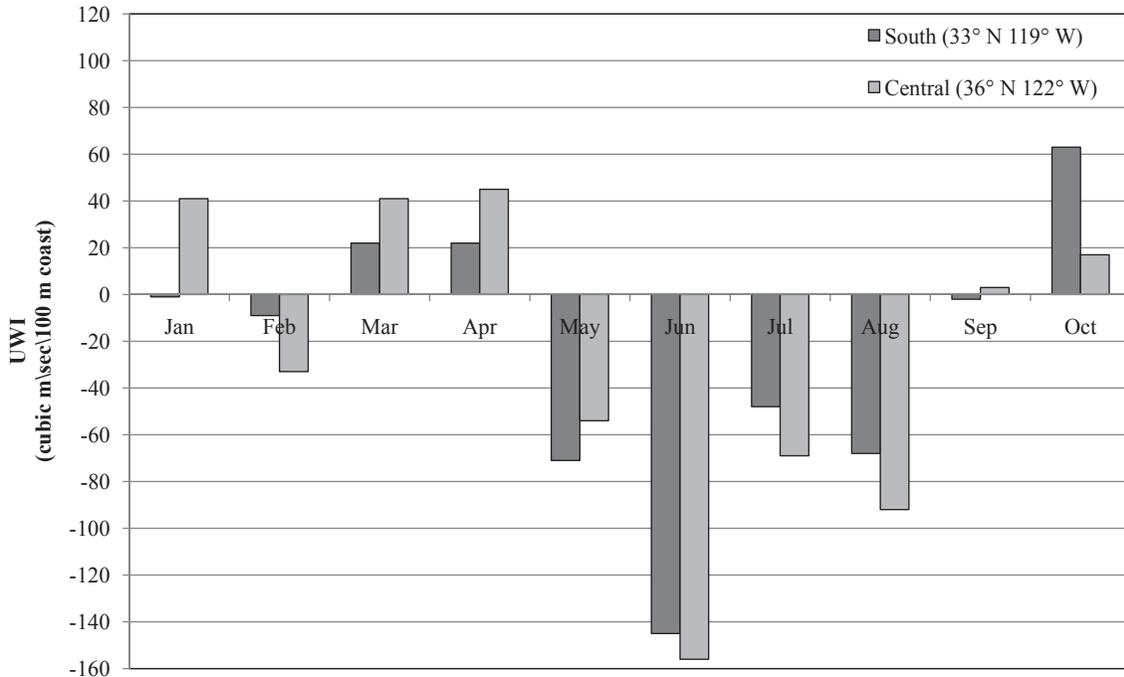
Figure 7. The monthly upwelling index (UWI) anomaly for the central and southern California coast in 2009. The baseline UWI anomaly was calculated for the years 1946 to 1986.
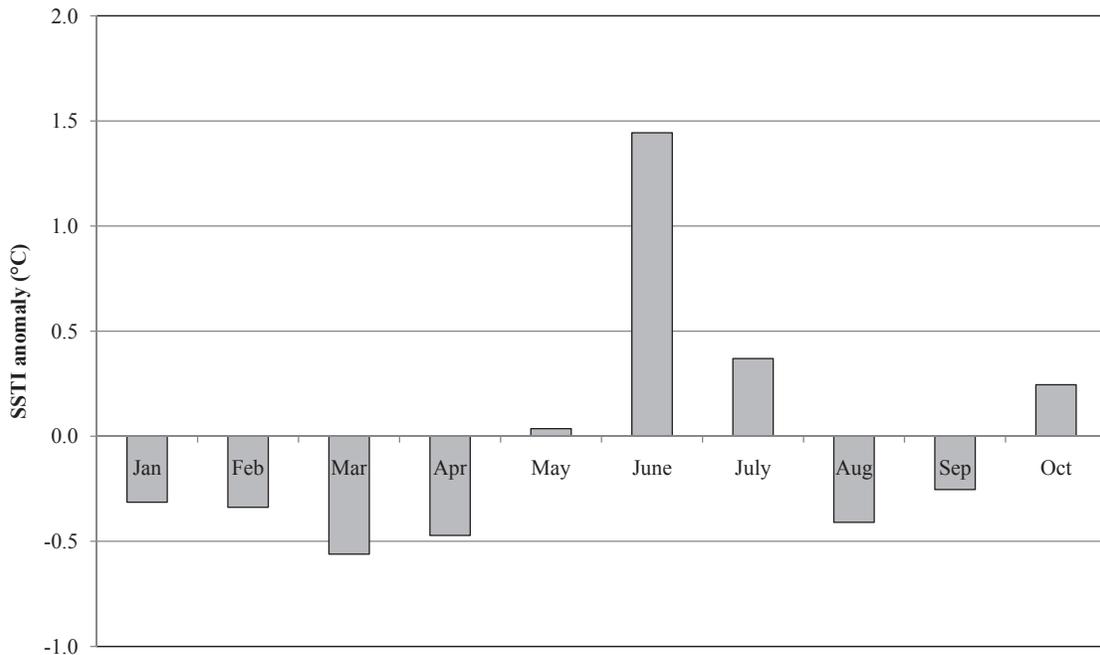
Figure 8. The monthly sea surface temperature index (SSTI) anomaly for seven buoys along the central California coast in 2009. The baseline SSTI anomaly is based on monthly means summarized for 1994–1996 and 1998–2008.

Oceanographic Indices

In 2009, the CCS experienced strong positive upwelling between January and April indicated by positive UWI anomalies (fig. 7). This is the normal pattern in the spring for the CCS. In May the central (36°N 122°W) and south (33°N 119°W) regions transitioned to a negative upwelling pattern indicated by negative UWI anomalies. The most negative UWI anomaly occurred in June. Upwelling anomalies remained negative through August, shifting to a positive upwelling pattern in September and October. SSTI anomalies were mostly negative during the strong positive upwell-

TABLE 1

Prey fish taxa consumed by California sea lions at San Miguel Island, California in July and early August in 2000, 2001, 2002, 2004, 2005 (Early 2000s) and 2009. Prey taxa were identified from hard parts recovered from fecal samples. '*n*' is number of fecal samples. '%FO' is percent Frequency of Occurrence. Primary prey indicated in bold. Shaded taxons are new species identified in the diet of California sea lions in the Channel Islands.

	% FO					
	Early 2000s					
Prey taxon	2000 (*n*=63)	2001 (*n*=61)	2002 (*n*=86)	2004 (*n*=91)	2005 (*n*=86)	2009 (*n*=44)
Rockfish, *Sebastes* spp.	7.9	13.1	15.1	6.6	27.9	45.5
Northern anchovy, *Engraulis mordax*	68.3	23.0	10.5	67.0	39.5	25.0
Pacific sardine, *Sardinops sagax*	14.3	1.6	36.0	76.9	46.5	15.9
Pacific hake, *Merluccius productus*	55.6	80.3	40.7	28.6	55.8	13.6
Pacific saury, *Cololabis saira*	15.9	6.6	14.0	9.9	22.1	9.1
Jack mackerel, *Trachurus symmetricus*	1.6	9.8	0.0	2.2	10.5	6.8
Northern lampfish, *Stenobrachius leucopsarus*	0.0	0.0	0.0	6.6	1.2	9.1
Pacific sanddab, *Citharichthys sordidus*	0.0	0.0	1.2	2.2	0.0	6.8
Spotted cuskeel, *Chilara taylori*	0.0	0.0	2.3	0.0	1.2	4.5
Sculpin, Cottidae	0.0	0.0	0.0	0.0	0.0	4.5
Slender barricudina, *Lestidiops ringens*	0.0	0.0	0.0	0.0	0.0	4.5
Blackbelly eelpout, *Lycodopis pacifica*	0.0	0.0	0.0	0.0	0.0	4.5
Dover sole, *Microstomus pacificus*	0.0	0.0	0.0	1.1	1.2	4.5
California laternfish, *Symbolophorus californiensis*	0.0	3.3	1.2	2.2	2.3	4.5
Blue lanternfish, *Tarletonbeania crenularis*	0.0	3.3	1.2	2.2	0.0	4.5
Sablefish, *Anoplopoma fimbria*	0.0	0.0	0.0	0.0	0.0	2.3
Surf perch, Embiotocidae	0.0	0.0	0.0	0.0	0.0	2.3
Rex sole, *Glyptocephalus zachirus*	0.0	0.0	0.0	0.0	0.0	2.3
Goby, Gobiidae	0.0	0.0	0.0	1.1	0.0	2.3
English sole, *Parophrys vetulus*	0.0	0.0	0.0	0.0	0.0	2.3
Pacific blacksmelt, *Bathylagus pacificus*	0.0	0.0	0.0	0.0	1.2	0.0
Herring, Clupeidae	0.0	1.6	0.0	0.0	1.2	0.0
Pacific hagfish, *Eptatretus stoutii*	0.0	1.6	0.0	0.0	0.0	0.0
Greenling, Hexagrammidae	0.0	1.6	0.0	0.0	0.0	0.0
California smoothtongue, *Leuroglossus stilbius*	6.3	0.0	2.3	3.3	2.3	0.0
Duckbill barracudina, *Magnisudis atlantica*	1.6	0.0	0.0	0.0	0.0	0.0
Laternfish, Myctophidae	0.0	1.6	0.0	0.0	0.0	0.0
Smelt, Osmeridae	0.0	1.6	0.0	0.0	0.0	0.0
Pacific pompano, *Peprilus simillimus*	0.0	1.6	0.0	0.0	1.2	0.0
Righteye flounder, Pleuronectidae	0.0	0.0	0.0	0.0	1.2	0.0
Plainfin midshipmen, *Porichthys notatus*	0.0	0.0	1.2	0.0	0.0	0.0
Sand sole, *Psettichthys melanostictus*	0.0	1.6	0.0	0.0	0.0	0.0
Pacific mackerel, *Scomber japonicus*	1.6	6.6	0.0	0.0	0.0	0.0
Queenfish, *Seriphus politus*	0.0	1.6	1.2	0.0	0.0	0.0
Spiny dogfish, *Squalus acanthias*	3.2	0.0	0.0	0.0	0.0	0.0
Prickleback, Stichaeidae	0.0	1.6	0.0	0.0	0.0	0.0

TABLE 2

General linear model results comparing FO in 2009 for each diet component and primary fish taxon from California sea lion fecal samples against each year from the Early 2000s samples. Model for each diet component or fish taxon was $y = 1+$ year where 2009 was the intercept. Results are significant at $\alpha =< 0.05$ and '−' is less than 2009, '+' is greater than 2009, or '0' is no difference from 2009.

	Early 2000s				
	2000	2001	2002	2004	2005
Diet Composition					
Mixed fish and cephalopod	0	+	0	−	0
Fish only	−	−	0	+	0
Cephalopod only	−	−	−	−	−
Primary Fish Taxa					
Rockfish (*Sebastes* spp.)	−	−	−	−	−
Northern anchovy (*Engraulis mordax*)	+	0	−	+	0
Pacific sardine (*Sardinops sagax*)	0	−	+	+	+
Pacific hake (*Merluccius productus*)	+	+	+	0	+
Pacific saury (*Cololabis saira*)	0	0	0	0	0
Jack mackerel (*Trachurus symmetricus*)	0	0	0	0	0

TABLE 3

Diet composition and primary fish taxa consumed by California sea lions at San Miguel Island, California in July and early August in 2000, 2001, 2002, 2004, 2005 (Early 2000s) and 2009. Prey taxa were identified from hard parts recovered from fecal samples. '%FO' is percent Frequency of Occurrence. Statistics are from Analysis of Variance (ANOVA) tests and compare 2009 to Early 2000s samples.

| | % FO | | | | |
| | | Early 2000s | | | |
	2009	Mean	S. E.	P	$F_{0.05,5}$
Diet Composition					
Mixed fish and cephalopod	38.5	50.5	8.8	0.606	0.313
Fish only	30.7	40.9	10.3	0.707	0.163
Cephalopod only	30.8	8.6	2.9	0.034	10.112
Fish Taxons					
Rockfish (*Sebastes* spp.)	45.5	14.1	3.8	0.028	11.405
Northern anchovy (*Engraulis mordax*)	25.0	41.6	11.6	0.589	0.345
Pacific sardine (*Sardinops sagax*)	15.9	35.1	13.1	0.582	0.357
Pacific hake (*Merluccius productus*)	13.6	52.2	8.7	0.144	3.290
Pacific saury (*Cololabis saira*)	9.1	13.7	2.7	0.520	0.497
Jack mackerel (*Trachurus symmetricus*)	6.8	4.8	1.7	0.733	0.134

TABLE 4

Top linear models predicting the annual mortality rate of 5-week old California sea lion pups at San Miguel Island, California, with explanatory variables of year, monthly sea surface temperature index (SSTI) anomaly, and monthly upwelling index anomaly at 36°N 122°W (UWI36N) and 33°N 119°W (UWI33N).

Model	Parameters	F-statistic	df	P	Adjusted R^2	AICc
obsmr ~Year+SSTI.Jun	3	9.197	10	0.005	0.577	–14.971
obsmr ~SSTI.Jun+UWI36N.Jun	3	7.484	10	0.010	0.519	–13.299
obsmr ~SSTI.Jun	2	8.629	11	0.014	0.389	–12.400
obsmr ~Year+SSTI.Jun+UWI36N.Jun	4	6.013	9	0.016	0.556	–11.371
obsmr~Year+SSTI.JunJul	3	5.590	10	0.024	0.433	–11.160
obsmr ~Year+SSTI.Jun+UWI33N.Jun	4	5.564	9	0.020	0.533	–10.707
obsmr ~SSTI.Jun+UWI33N.Jun	3	5.027	10	0.031	0.402	–10.450
obsmr ~Year+SSTI.MayJun	3	3.407	10	0.074	0.286	–8.1599
obsmr ~Year+SSTI.MayJul	3	3.330	10	0.078	0.280	–8.0390

ing between January and April. The negative upwelling between May and July resulted in warmer than average SSTI in June and July, with the greatest positive SSTI anomaly occurring in June. Negative SSTI anomalies returned in August and September as upwelling increased along the coast and SSTs cooled (fig. 8).

Model of Early Pup Mortality and Oceanographic Indices

The model that best explained the annual variability in pup mortality rates at 5 weeks of age between 1997 and 2009 included year and June SSTI as explanatory variables (tab. 4). The 10 best models included June SSTI. Pup mortality increased with increasing positive June SSTI anomalies (fig. 9). The highest positive June SSTI anomalies (> 1.4°C) in the ENSO year of 1998 and the unusually warm year of 2009 were associated with the highest mortality rates (fig. 9). Other suitable models included June SSTI only and June UWI at 36°N 122°W and June SSTI as explanatory variables for annual pup mortality.

DISCUSSION

The unprecedented mortality of California sea lion pups born at San Miguel Island, California and the record number of emaciated weaned pups that stranded along the central California coast in 2009 were associated with anomalous oceanographic conditions along the central California coast between May and August 2009. The conditions only persisted for 4 months but the timing and magnitude of the event relative to weaning and birthing of California sea lion pups resulted in 80% mortality of the 2009 cohort by 3.5 months of age at San Miguel Island. Although strandings of weaned pups occur regularly along the California coast during the spring and summer, in 2009, strandings were high throughout California. Along southern California coasts, more than 400 strandings occurred (J. Cordaro, NOAA, NMFS, personal communication) and we documented 640 strandings for central and northern California, almost 11 times the average between 1997 and 2008.

The positive upwelling and cooler SSTs along the central coast between January and April 2009 were
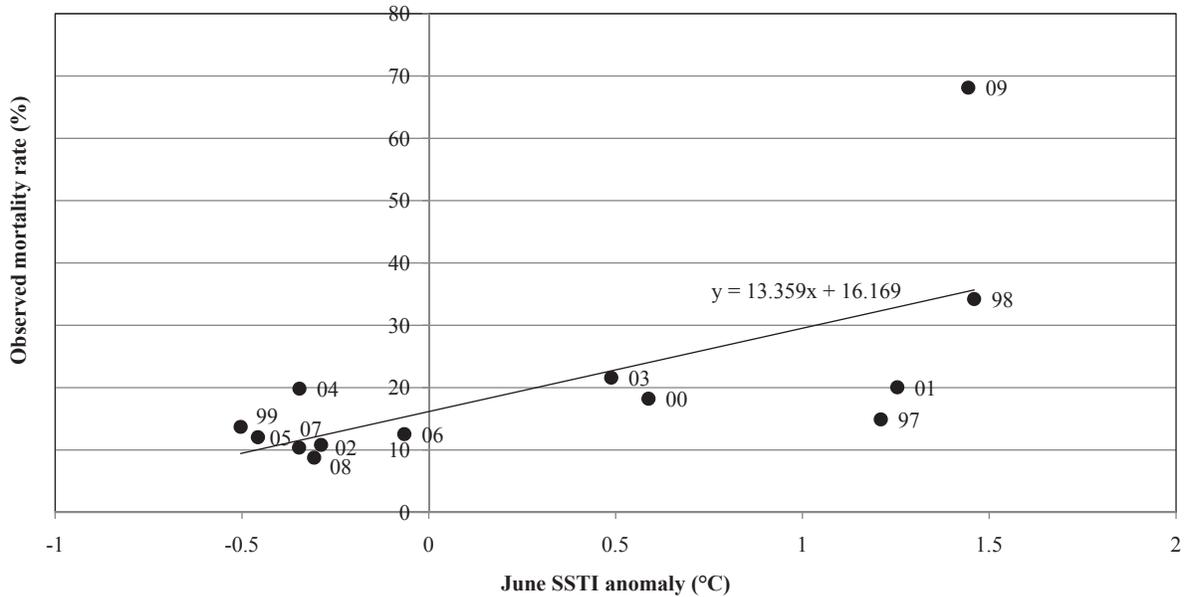
Figure 9. The relationship between observed California sea lion pup mortality at 5 weeks of age at San Miguel Island, California, and the June SSTI anomaly for the central and southern California Current System (CCS) between 1997 and 2009.

within the normal pattern for the CCS (Bograd et al. 2009). This likely lead to adequate prey availability for pregnant California sea lion females and resulted in normal patterns in the timing of births and pup production. We would have expected a later median birth date, a protracted birthing season, and lower pup production in addition to pup mortality if pregnant females had had difficulty finding enough food to support gestation and late lactation. When the oceanographic conditions transitioned to negative upwelling patterns and warmer SSTs in the summer, mothers responded with long foraging trips averaging 7 days, up to 4 days longer than trips in the 1980s (Feldkamp et al. 1989; Antonelis et al. 1990), that approached the maximum duration for which pups survive without nursing (9 days, Heath 1989). Although the methods of measuring trip duration were different among the studies (telemetry in the earlier studies vs. visual observation in this study), the magnitude of the difference was too great to be attributed to sampling method alone. Behavioral observations have been shown to underestimate trip duration by up to 7% in Antarctic fur seals (*Arctocephalus gazella*) (Boyd et al. 1991) and overestimate duration by 3.4% in Australian sea lions (*Neophoca cinerea*) (Higgins and Cass 1993) relative to telemetry derived durations. Biases of these magnitudes would not result in trip durations significantly different from those we observed. The longer foraging trips indicate that lactating females had difficulty finding sufficient prey or prey of adequate energetic value within their normal foraging range to energetically maintain themselves and sustain lactation. Because pups fast while their mother is away on foraging trips, repeated forag-

ing trips lasting up to 7 days likely resulted in a nutritional deficit for the pups such that they succumbed to starvation within the first months of life. The duration of visits ashore was not different from other studies at San Miguel Island (Antonelis et al. 1990). Thus, longer absences by females were not compensated by longer periods ashore for nursing.

The primary prey of California sea lion females in the summers of our study were similar to previous studies with fish and cephalopods comprising the diet and Pacific sardine, northern anchovy, Pacific hake and rockfish representing the primary fish taxons (Antonelis et al. 1984, Lowry et al. 1990, Lowry 1991, Melin et al. 2008). The increased FO of cephalopods in the diet in 2009 (30.8%) compared to the early 2000s (8.6%) indicates that cephalopods were more available to California sea lions than usual during the summer of 2009. The FO of the fish taxons in the diet also changed in 2009. Most notably, rockfish became the dominant fish taxon and the importance of Pacific hake, Pacific sardine and northern anchovy was considerably less than in the early 2000s. The increase in rockfish in 2009 could be due to increased abundance of rockfish due to strong year classes of rockfish in 2003 and 2006 (Field et al. 2007), or it could reflect reduced availability of sardine, anchovy and hake due to the anomalous ocean conditions in the summer. The preferred summer diet with high FO of sardine, anchovy and hake likely provides an energy rich diet that allows females to support lactation. The high pup mortality in 2009 suggests that the combination of longer foraging trips and a diet principally of rockfish and cephalopods did

not provide adequate energy for lactating females to support their pups.

The results of our model of pup mortality in which the SSTI in June predicted higher pup mortality, suggest that the response of prey to SST changes and the response of sea lions to a change in prey availability, are relatively immediate. For California sea lions, reduced prey availability or a diet of energetically inferior prey in June is likely to have a significant impact on pup survival because it may result in longer foraging trips for their mothers and possibly less energy transfer between mothers and pups at a time when the pups are solely dependent on their mothers for nutrition and have limited fasting capabilities.

The record number of emaciated weaned pups from the 2008 cohort that stranded along the central California coast in 2009 indicates that weaned pups had difficulty finding food in the summer shortly after they achieved independence from their mothers. Although weaning is a gradual process in California sea lions, dependent pups do not accompany their mothers to foraging areas (Melin et al. 2000). When pups are weaned, they are naïve to the location of foraging areas away from the colony and must learn to find them and to capture prey on their own. Weaned pups have limited physiological capabilities for diving and traveling (Fowler et al. 2006; Richmond et al. 2006) and thus, if they encounter poor foraging conditions before becoming proficient hunters, they may die from starvation.

Coastal upwelling processes are important determinants of local and regional SSTs which in turn affects the distribution and reproduction of marine species by influencing the distribution of their prey (Ainley et al. 1995; Ainley et al. 2005; Lluch-Belda et al. 2005; Wells et al. 2008). In 2009, the decreased upwelling along the central California coast produced warm, low nutrient water along the coast between May and August but the highest number of starving weaned pups and the highest pup mortality occurred during the period of the warmest SSTI and the most negative UWI anomalies in June 2009. This suggests that the response of California sea lions to the anomalous oceanographic conditions in 2009 was mediated through warmer SSTs that likely resulted in reduced availability of their prey. The association of changes in SSTs with prey availability and production or survival of predators has been documented for seabirds (Abraham and Sydeman 2004; Ainley et al. 2005; Sydeman et al. 2006; Mills et al. 2007; Wells et al. 2008) and marine mammals (Melin 2002; Beauplet et al. 2005; Weise et al. 2006). Though we did not conduct prey distribution studies in 2009, we observed that northern fur seals (*Callorhinus ursinus*) that breed at San Miguel Island at the same time as California sea lions and feed on similar prey (Antonelis et al. 1990) did

not experience massive mortality of their pups in 2009. Northern fur seals feed offshore in the pelagic zone during the summer (Antonelis et al. 1990) unlike California sea lions that feed in coastal waters (Antonelis et al. 1990; Melin and DeLong 2000). This observation leads us to hypothesize that the primary prey moved offshore or northward in 2009 and was less available to lactating sea lion females due to the anomalous oceanographic patterns between May and August 2009. Future analyses will combine fishery landings data and fish larvae abundance surveys from the CalCOFI cruises in July 2009 within the foraging range of California sea lions to test this hypothesis.

ACKNOWLEDGMENTS

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