CALIFORNIA SEA LIONS: AN INDICATOR FOR INTEGRATED ECOSYSTEM ASSESSMENT OF THE CALIFORNIA CURRENT SYSTEM

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ABSTRACT

We examined the annual number of pups born, pup mortality, and pup weights of California sea lions (*Zalophus californianus*) at San Miguel Island, California, and related them to large and small-scale oceanographic indices in the central California Current System (CCS) between 1997 and 2011. Annual variability in the number of pups born and pup mortality was best explained by the mutlitvariate ENSO index (MEI) that tracks the El Niño/La Niña cycle. Annual variability in average pup weights was best explained by a sea surface temperature anomaly index (SSTA); average pup weights were lower in years when the SSTA was greater than 1˚C above normal. We demonstrated that California sea lions are sensitive to large and small-scale changes in ocean conditions through changes in their reproductive success, pup growth, and pup mortality. Therefore, California sea lions are an ideal indicator species for the IEA of the CCS.

INTRODUCTION

Integrated ecosystem assessment (IEA) is the scientific foundation that supports ecosystem-based management (Levin et al. 2009). A central component of IEA is the identification of indicator species that respond to changes in the ecosystem. In the California Current System (CCS), large-scale global processes like the Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and El Niño Southern Oscillation (ENSO) as well as small-scale processes like localized disruption of seasonal upwelling can alter the trophic dynamics on time scales of months, years, or decades (Hayward 1997; McGowan et al. 2003; Goericke et al. 2007; Bjorkstedt et al. 2010; King et al. 2011). In the CCS, the atmospheric forcing associated with the PDO and NPGO controls decadal patterns in upwelling and results in regionally variable coastal upwelling conditions that affect primary and secondary marine productivity and consequently, the distribution of fishes and other higher trophic level marine organisms. Thus, suitable indicator species for the CCS must be sensitive to marine ecosystem changes at various spatial and temporal scales. An indicator species should be directly observable, have a historical time series of data that includes periods of large- and small-scale environmental changes, be sensitive to changes in the ecosystem, and have traits that respond to and that can be measured in relation to the ecosystem processes of interest (Rice and Rochet 2005). Upper trophic level marine predators often make good indicator species because annual changes in population parameters, such as births, mortality, and growth, are often linked to oceanographic changes (e.g., production of chlorophyll and zooplankton) that affect the distribution and availability of lower trophic level prey (e.g., euphausiids, fishes, cephalopods) (Ainley et al. 2005; Beauplet et al. 2005; Foracada et al. 2005; Reid and Forcada 2005; Reid et al. 2005; Wells et al. 2008).

California sea lions (*Zalophus californianus*) are upper trophic level marine predators that are abundant and permanent residents of the CCS. Their range extends from northern Mexico to Canada and much of their life history has evolved to take advantage of the high ocean productivity in the CCS. Weaning and reproduction occur during late spring and early summer, respectively, during the peak upwelling period in the CCS when primary productivity is at its maximum (Bograd et al. 2009). California sea lion females give birth to a single pup between May and June that they provision through lactation. Lactation usually lasts 11 months during which time females are central-place foragers, alternating 2–5 day foraging trips to sea with 1–2 day nursing visits to the colony (Melin et al. 2000). Lactating females exploit the continental shelf, slope, and offshore regions of the central and southern CCS throughout the year (Kuhn 2006; Melin et al. 2008), making more than 60 foraging trips between the California Channel Islands and Monterey Bay, California. Their large foraging area and diving capabilities give them access to a diverse prey assemblage resulting in a diet that includes over 30 taxa of fish and cephalopods (Antonelis et al. 1990; Lowry et al. 1990; Melin et al. 2010).

Over the past 40 years, population parameters of California sea lions have shown annual variability associated with large- and small-scale oceanographic events. The populations breeding in the California Channel Islands off the southern coast of California experienced significant declines in births, increased pup mortality, lower mean pup weights, and changes in the diet in response to the warm oceanographic conditions associated with the El Niño phase of ENSO events in 1982–83 (DeLong et al. 1991), 1992–93 (DeLong and Melin 2000), and 1997–98 (Weise and Harvey 2008; Melin et al. 2010). The population effects lasted for 1 to 4 years (Lowry and Maravilla-Chavez 2005). Furthermore, California sea lions are also sensitive to regional and localized changes in their foraging environment that affect their prey base (Weise et al. 2006; Weise and Harvey 2008). In 2009, a brief collapse of the summer seasonal upwelling along the central California coast (Bjorkstedt et al. 2010) resulted in an unprecedented level of California sea lion pup mortality, a dramatic change in the adult female diet, and contributed to a reduction in the number of births in the following year (Melin et al. 2010). The impact of these anomalous oceanographic events on the California sea lion population are presumably meditated through their affect on sea lion prey availability (i.e., distribution, abundance), but it is difficult to measure prey availability directly. Therefore indices of ocean conditions like the PDO, NPGO, upwelling, and sea surface temperatures that affect distribution and abundance of prey can be used as proxies for prey availability to California sea lions and consequently, may explain annual variability in California sea lion population indices.

A reduction in prey available to lactating California sea lion females has the greatest population effect because it affects reproduction and survival of pups. When prey is scarce, lactating females expend more energy to meet the demands of reproduction by foraging farther from the colony and/or diving deeper presumably in response to changes in the spatial distribution of their prey (Melin et al. 2008). More importantly, movement of prey outside the normal adult female foraging range results in longer foraging trips (Melin et al. 2008), which may result in slower growth or starvation of the pup if the foraging trip durations exceed the pup's fasting capability. In addition, because lactating females are usually also pregnant during nine months of the 11-month lactation period, a diet that is insufficient to support both lactation and gestation may result in the resorption of the fetus or a premature birth. Given the relationships between ocean conditions, prey availability, and California sea lion behavior, we used regional and local oceanographic and adult female diet indices as explanatory variables in models of the annual number of pups born, pup mortality, and pup weight (as an index of growth) of California sea lions at San Miguel Island, California to 1) describe the relationship between annual variability in the marine environment and California sea lion population indices, and 2) determine if California sea lions could be used as an indicator species in the IEA of the CCS.

METHODS

Oceanographic Indices

PDO, NPGO, and ENSO. The PDO signal is strongest north of 38°N, the NPGO is strongest south of 38°N (Di Lorenzo et al. 2008), and the ENSO signal varies depending on the strength of the event at the equator (King et al. 2011) but all three indices are related and affect the CCS (King et al. 2011). So, we explored relationships between these indices and California sea lion population parameters. For each year between 1997 and 2011, monthly values for the PDO (http://jisao.washington.edu/pdo/PDO.latest), NPGO (http://www.o3d.org/npgo/npgo.php), and ENSO (multivariate ENSO index (MEI), http://www.esrl.noaa.gov/psd/enso/mei/table.html) were averaged for: 1) October through the following June (average gestation period) for models explaining trends in pup births, 2) June and July for models evaluating pup mortality up to 5 weeks of age, and 3) June through September for models exploring variability in pup mortality and pup weights at 14 weeks of age. Because the MEI is measured at the equator, the index was lagged 3 months, after testing lags of 0 to 6 months, based on the highest positive correlation between the average MEI values and local sea surface temperatures in lactating female sea lion foraging areas in the CCS (e.g., MEI value at the equator in January was assigned the CCS MEI value in April).

Local Upwelling and Sea Surface Temperature. Large-scale oceanographic patterns affect local ocean conditions in the CCS through changes in the timing, strength, and characteristics of upwelling and changes in sea surface temperature that affect the distribution of sea lion prey over shorter time periods (i.e., weeks or months) and may have more immediate effects on California sea lion population indices than large-scale processes. We used upwelling and sea surface temperature indices to investigate the effect of small-scale oceanographic conditions on California sea lion population and diet indices. The monthly coastal upwelling index at 33°N 119°W (UWI33) and 36°N 122°W (UWI36) (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html) between 1997 and 2011 was used as an index of regional monthly ocean productivity along the central California coast (Schwing et al. 2006). These two locations were the centers of 3 x 3 degree grids for which the upwelling index was computed and encompassed the foraging range of lactating female California sea lions (Melin and DeLong 2000) (fig. 1). Positive values of the UWI are generally associated with higher than normal ocean productivity and negative values are associated with lower than normal productivity in the CCS (Schwing et al. 1995). The baseline index was calculated from monthly means of

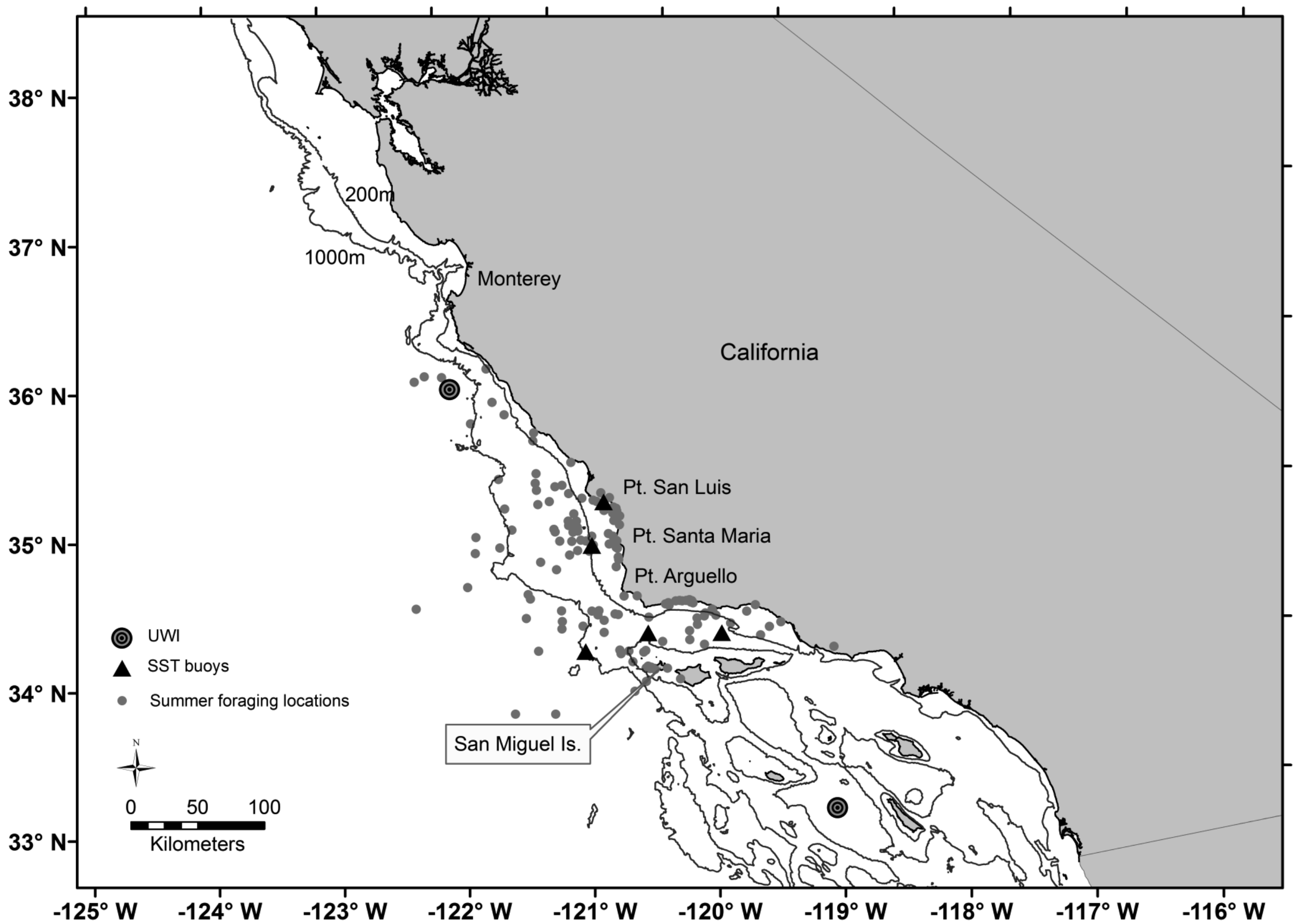

Figure 1. Locations of upwelling anomaly index sites and sea surface temperature buoys used for upwelling index (UWI) and sea surface temperature anomaly index (SSTA) within the summer foraging range of California sea lions from San Miguel Island, California. Data are from Melin and DeLong 2000 for California sea lion females in June–August 1995.

upwelling between 1946 and 1986. The monthly upwelling anomalies within each year between 1997 and 2011 were the difference between the baseline mean and the annual monthly mean.

For a more localized indicator of environmental conditions, we used sea surface temperature (SST) as a proxy for ocean productivity. Warmer SSTs are usually associated with low ocean productivity and cool SSTs with high productivity. We calculated a daily mean SST from five buoys (http://www.ndbc.noaa.gov/rmd.shtml) along the central California coast that overlapped with the foraging range of lactating female sea lions (fig. 1). A monthly baseline SST was calculated from the daily mean values for each buoy for the periods 1994 to 1996 and 1998 to 2011. 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, we subtracted the baseline monthly SST from the mean SST value for each month to construct a time series of monthly anomalies (SSTA). As for the large-scale indices, the monthly UWI and SSTA indices were averaged for: 1) November to the following June (average gestation period) for models explaining trends in pup births, 2) June and July for models evaluating pup mortality up to 5 weeks of age, and 3) June to September for models exploring variability in pup mortality and pup weights at 14 weeks of age.

California Sea Lion Population Indices

Study Site. San Miguel Island, California (34.03˚N, 120.4˚W), is one of the largest colonies of California sea lions, representing about 43% of the U.S. breeding population (calculated from Caretta et al. 2007). As such, it is a useful colony to measure trends and population responses to changes in the marine environment. The Point Bennett Study Area (PBSA) represents about 50% of the births that occur on San Miguel Island and provides a good index of trends for the entire colony. This site has been used as a long-term index site since the 1970s for measuring population parameters and we used this site for data on the number of pups born, pup mortality, and weights of pups between 1997 and 2011. We limited our data set to 1997–2011 and to the PBSA because this study area within this time series has the most complete data for all the parameters of interest for this study.

Pup Mortality. Pup mortality was assessed to calculate morality at 5 weeks of age, 14 weeks of age, and the total number of pups born. Pup mortality surveys conducted every 2 weeks from late June to the end of July were used as an index of pup mortality at 5 weeks of age and to calculate total births for the PBSA. A final survey was conducted the last week of September to estimate pup mortality at 14 weeks of age. On each survey, 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 or 14 weeks of age. Cumulative pup mortality rate was calculated as the proportion of the number of pups born in each year that died by 5 weeks of age or 14 weeks of age of the total number of pups born in each year.

Number of Births. Live pups were counted after all pups were born (between 20–30 July) each year. Observers walked through the PBSA, moved adults away from pups, and then counted individual pups. A mean of the number of live pups was calculated from the total number of live pups counted by each observer. The total number of births 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.

Pup Weights. Between 310 and 702 pups were selected from large groups of California sea lions hauled out in Adams Cove (part of the PBSA) over 4–5 days in September or October in each year (when about 14 weeks old). Pups were sexed, weighed, tagged, branded, and released. Because the weighing dates were not the same in each year, we standardized the weights to a 1 October weighing date. A mean daily weight gain rate times the number of days from the weighing date to 1 October was added or subtracted from the pup weight based on the number of days before (–) or after (+) 1 October that the pup was weighed. The number of days between 1 October and the actual weighing day was included as a parameter (days) in models to describe annual variability in pup weights.

Adult Female Diet. We collected fecal samples from adult female California sea lion haul out areas in the PBSA in June through September in 2000–03, 2005, and 2009–11 to examine the diet and develop diet indices to include in the models of pup weights. Sample processing followed Orr et al. 2003. Fish bones, fish otoliths, and cephalopod beaks were recovered from the samples and identified to family, genus, or species. Rockfish (*Sebastes* spp.) otoliths were from juvenile fish and badly eroded with no identifiable fine structures to reliably determine species, so to be conservative with identification they were identified to the genus level. When only upper cephalopod beaks were present in the sample, they were only identified to genus because many upper beaks within a genus are too similar to identify to species. We used three indices to describe diet: 1) frequency of occurrence (FO) is a measure of the percentage of fecal samples in which a prey taxon occurred, 2) split-sample frequency of occurrence (SSFO) is a measure of the percentage of occurrences for each prey taxon from the total count of all prey taxa found in a sample year; this index was used in the Principal Components Analysis (PCA), and 3) species richness is a measure of diet diversity based on the number of species present within each scat. All the diet indices are based on the presence or absence of a taxon in a fecal sample and are only a relative measure of prey occurrence because of biases associated with extrapolating from fecal contents to meal contents, biomass, or percent biomass of prey consumed by pinnipeds (Laake et al. 2002; Joy et al. 2006). The SSFO were used in PCA in R (R Core Development Team 2009) to develop a diet type index to explore if there were annual patterns in prey taxa found in the diet. The two diet indices, diet type and species richness, were used in models of pup weight at 14 weeks of age from the years for which diet data were available (2000–03, 2005, and 2009–11) to determine if adult female diet explained annual variability in pup weight.

Models

We used general linear models (pup births, 5-week pup morality, and 14-week pup mortality) and linear mixed-effects models (pup weights) in R (R Core Development Team 2009) to develop models to explore relationships between oceanographic and California sea lion population indices. A sequence of models was developed for each population index that included year and one or more of the oceanographic indices: PDO, NPGO, MEI (ENSO index), UWI33, UWI36, or SSTA. Pup weight models also included pup sex, days (days prior or after 1 October of actual weighing date), and cohort as explanatory fixed-effect variables. To accommodate potential random variation in mean pup weights within years and growth rates over the sampling period within each year, random effects of cohort (year) and batch (weighing dates within each year) on average weights (intercept) and growth rates (slope of batch) were included in the models. The best random effects model included a cohort and batch effect, so these random effects were included in all of the mixed-effects models.

A mean value was used for each oceanographic index that summarized the index values over the different seasonal periods because pup births (October to following June), pup weights (June through September), and pup mortality (June to July and June to September) are related to the cumulative energy transfer from mother to pup from birth to the time of weighing or death. Following Zuur et al. 2008, the Akaike Information Criterion adjusted for small sample sizes (AICc) was used to select the best model for each population parameter. We chose a model selection approach rather than a traditional step-wise hypothesis testing approach because it allows for a more objective process of inference that evaluates sources of variability in a biological context based on well-defined criteria and a strong fundamental basis (Burnham and Anderson 1998). Models separated by less than 4 in their AICc values were considered plausible for a given set of candidate models.

RESULTS

California Sea Lion Population Indices

Number of Births. Annual births in the PBSA at San Miguel Island between 1997 and 2011 ranged from a low of 8,603 to a high of 17,203 (table 1). The greatest annual declines occurred in 1998 (–44.1%), 2003 (–27.3%), and 2010 (–41.3%). We evaluated 11 models; the model with year and MEI_{OJ} was the best model to describe annual variability in pup births (B5; table 4). There was a negative trend in pup births over the time series (slope = –301.3, SE = 113.7) and a negative relationship between the number of births and average MEI between October and June the following year (slope = –2471.1, SE = 567.9). MEI_{OJ} values that were greater than 0.5 or less than 0.5 tended to be associated with the lowest and highest pup births, respectively (table 1). The next best models included two additive models with MEI_{OJ} and $UWI36_{OJ}$ (B10) or $UWI33_{OJ}$ (B11), and one model with year and $SSTA_{OJ}$ (B2) as variables (table 1). All of these models had very similar AICc values that were larger than the best model but also represent plausible explanations for the variability in the number of births among years (AICc values <4 from the best model).

Pup Mortality. Pup mortality that occurs in the first 5 weeks (early season mortality) is usually related to trauma or starvation. Mortality of 5-week-old pups was highest in 2009 (74%) and 1998 (40.9%) and lowest in 2008 (11.4%) (table 2). We evaluated 10 models for pup mortality at 5 weeks of age. The best model included only $SSTA_{JJ}$ as an important effect explaining year-to-year variation (EM4; table 4). Average pup mortality was 21.9% (SE = 6.6%) and a 1°C increase in the $SSTA_{JJ}$ increased mortality an average of 12% (SE = 5.4%). Other competitive models included models with $UWI36_{JJ}$ (EM6 and EM7), $UWI33_{JJ}$ (EM5 and EM8), alone or in combination with $SSTA_{JJ}$ (table 4).

Starvation and trauma continue to be major factors of mortality for older pups but disease becomes a significant mortality factor for pups 6 weeks and older (Lyons et al. 2005; Spraker et al. 2007). High pup mortality by 14 weeks of age occurred in 1998 (50.3%), 2001 (52.6%), and 2009 (80.3%) (table 3). Of 10 models, the best model estimated an average pup mortality of 35.3% (SE = 8.6%) and most of the variability was explained by a positive relationship between pup

TABLE 1
Total number of California sea lion pups born in the PBSA, San Miguel Island, California, 1997–2011, and mean values of oceanographic indices from October (year – 1) to the following June (year) (denoted with subscript OJ) used in models to evaluate annual variability in pup births. PDO_{OJ} = Pacific Decadal Oscillation, $NPGO_{OJ}$ = North Pacific Gyre Oscillation, MEI_{OJ} = multivariate ENSO index, $UWI33_{OJ}$ = Upwelling anomaly at 33°N 119°W, $UWI36_{OJ}$ = Upwelling anomaly at 36°N 122°W, $SSTA_{OJ}$ = Sea surface temperature anomaly.

		Oceanographic indices					
Year	Number of births	PDO_{OJ}	$NPGO_{OJ}$	MEI_{OJ}	$UWI33_{OJ}$	$UWI36_{OJ}$	$SSTA_{OJ}$
1997	16,670	0.61	–1.02	0.29	0	33	0.43
1998	9,325	1.02	0.58	2.24	–34	–17	2.40
1999	17,203	–0.78	1.50	–0.89	30	71	–0.64
2000	17,106	–1.07	1.84	–0.78	–19	2	–0.27
2001	15,333	–0.23	2.36	–0.39	–16	28	–0.05
2002	16,220	–0.74	1.67	0.19	5	44	–0.40
2003	11,819	1.24	1.44	0.68	13	16	0.02
2004	12,474	0.41	0.32	0.30	–35	–7	–0.09
2005	11,343	0.53	–0.93	0.65	–20	–9	0.48
2006	14,723	0.00	–0.28	–0.31	–3	1	–0.27
2007	15,557	–0.14	0.41	0.47	43	57	–0.27
2008	11,492	–1.20	1.45	–0.92	13	36	–0.79
2009	14,651	–1.36	1.07	–0.29	–16	–2	0.16
2010	8,603	0.25	1.86	0.89	14	3	0.43
2011	15,925	–0.89	1.24	–1.25	–6	–5	–0.52

TABLE 2
Pup mortality rate at 5 weeks of age of California sea lion pups born in the PBSA, San Miguel Island, California, 1997–2011, and mean values of oceanographic indices from June through July (denoted with subscript JJ) used in models to evaluate annual variability in mortality. PDO_{JJ} = Pacific Decadal Oscillation, $NPGO_{JJ}$ = North Pacific Gyre Oscillation, MEI_{JJ} = multivariate ENSO index, $UWI33_{JJ}$ = Upwelling anomaly at 33°N 119°W, $UWI36_{JJ}$ = Upwelling anomaly at 36°N 122°W, $SSTA_{JJ}$ = Sea surface temperature anomaly.

		Oceanographic indices					
Year	Pup mortality rate	PDO_{JJ}	$NPGO_{JJ}$	MEI_{JJ}	$UWI33_{JJ}$	$UWI36_{JJ}$	$SSTA_{JJ}$
1997	18.9	2.34	–0.86	2.48	–10	47	1.38
1998	40.9	–0.03	0.26	0.74	–88	–31	1.52
1999	17.5	–1.19	1.64	–0.46	30	92	–0.24
2000	22.9	–0.76	1.88	–0.24	–21	29	0.35
2001	25.0	–1.10	1.92	0.07	–18	83	0.59
2002	13.9	–0.54	1.49	0.70	23	115	–0.14
2003	26.8	0.61	0.99	0.02	79	102	–0.10
2004	24.8	0.03	0.59	0.36	–83	–64	–0.08
2005	15.4	0.70	–1.14	0.44	–71	–52	–0.78
2006	16.0	0.48	0.05	0.55	–86	–24	0.07
2007	13.4	0.22	1.50	–0.30	–41	–41	–0.47
2008	11.4	–1.72	1.61	0.06	–78	–62	0.05
2009	74.0	–0.63	0.71	0.88	–97	–113	0.83
2010	23.8	–0.85	1.39	–0.79	12	33	–0.84
2011	15.5	–1.49	1.33	–0.19	–14	–6	–0.32

TABLE 3
Pup mortality rate and mean pup weight at 14 weeks of age of California sea lion pups born in the PBSA, San Miguel Island, California, 1997–2011 and mean values of oceanographic and diet indices from June through September (denoted with subscript JS) used in models to evaluate annual variability in mortality and weight. PDO_{JS} = Pacific Decadal Oscillation, $NPGO_{JS}$ = North Pacific Gyre Oscillation, MEI_{JS} = multivariate ENSO index, $UWI33_{JS}$ = Upwelling anomaly at 33°N 119°W, $UWI36_{JS}$ = Upwelling anomaly at 36°N 122°W, $SSTA_{JS}$ = Sea surface temperature anomaly, sprich = Species richness in diet, diet4 = Four diet types. A '–' indicates no data for that year.

		Pup weight													
		Females			Males			Oceanographic Indices						Diet indices	
Year	Pup mortality rate	n	Mean (kg)	SE	n	Mean (kg)	SE	PDO_{JS}	$NPGO_{JS}$	MEI_{JS}	UWI 33_{JS}	UWI 36_{JS}	$SSTA_{JS}$	sprich	diet type
1997	29.6	347	14.4	0.14	194	17.2	0.15	2.38	–0.74	2.67	–9	24	2.17	–	–
1998	50.3	409	12.6	0.16	293	15.3	0.17	–0.41	0.21	0.18	–72	–18	1.98	–	–
1999	23.7	302	18.3	0.14	200	21.0	0.14	–1.25	1.51	–0.63	26	55	–0.72	–	–
2000	33.7	324	17.1	0.14	183	19.8	0.14	–1.02	1.62	–0.22	–18	27	0.25	2.80	2
2001	52.6	329	15.9	0.12	206	18.6	0.12	–1.12	1.91	0.05	5	75	0.02	2.51	2
2002	32.8	334	17.0	0.12	180	19.7	0.12	–0.05	1.16	0.76	17	75	–0.79	2.87	1
2003	41.8	393	18.4	0.11	275	21.1	0.12	–0.49	0.91	0.19	93	86	–0.45	4.00	3
2004	46.4	304	20.9	0.18	198	23.6	0.18	0.38	0.56	0.47	–84	–63	0.29	–	–
2005	37.6	301	20.2	0.18	199	22.9	0.18	0.26	–1.09	0.38	–42	–25	–0.55	2.61	1
2006	25.6	275	19.0	0.16	231	21.7	0.16	–0.19	–0.01	0.68	–48	–16	0.22	–	–
2007	25.1	308	19.1	0.16	204	21.8	0.17	0.11	1.41	–0.54	–33	–42	–0.35	–	–
2008	14.8	195	17.8	0.24	115	20.5	0.24	–1.71	1.97	–0.16	–65	–57	0.47	–	–
2009	80.3	298	14.8	0.19	216	17.5	0.19	–0.20	0.87	0.87	–66	–79	0.39	1.99	4
2010	30.2	234	17.1	0.17	190	19.8	0.17	–1.18	1.30	–1.34	0	21	–1.39	3.04	2
2011	24.8	239	14.8	0.16	108	17.5	0.17	–1.66	1.39	–0.41	–8	12	–0.51	3.08	2

mortality rates and MEI_{JS} (LM2; table 4), with positive MEI values associated with the higher pup mortality. However, models with $SSTA_{JS}$ (LM4), $UWI33_{JS}$ (LM5), $UWI36_{JS}$ (LM6), and PDO_{JS} (LM1) were also considered plausible models for this parameter (table 4). $SSTA_{JS}$ had a positive relationship with pup mortality; $SSTA_{JS}$ greater than 1°C were associated with the highest pup mortality. The UWI models showed a negative relationship between pup mortality and average UWI values with negative UWI values being associated with higher pup mortality.

Pup Weights. Average weights of 14-week-old pups were quite variable over the 15-year period (table 3). Of 38 models evaluated for annual variability in pup weights, the best model included random intercepts for cohort and batch (day of weighing), and fixed sex-specific intercepts for growth rates (sex:days) and average $SSTA_{JS}$ (sex:$SSTA_{JS}$) (PW6; table 4). The aver-

TABLE 4
Models evaluating the relationships between California sea lion population indices and oceanographic indices in the CCS between 1997 and 2011. 'np' is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample size (n=15).

California sea lion population index	Model #	Model Parameters[1]	np	AICc
Total births	B5	Year+MEI_{OJ}	3	274.82
	B10	Year+MEI_{OJ}+$UWI36_{OJ}$	4	277.46
	B11	Year+ MEI_{OJ}+$UWI33_{OJ}$	4	277.65
	B2	Year+$SSTA_{OJ}$	3	277.83
Pup mortality at 5 weeks old				
	EM4	$SSTA_{JJ}$	2	–8.61
	EM7	$SSTA_{JJ}$+$UWI36_{JJ}$	3	–7.79
	EM6	$UWI36_{JJ}$	2	–6.34
	EM8	$SSTA_{JJ}$+$UWI33_{JJ}$	3	–6.00
	EM5	$UWI33_{JJ}$	2	–5.65
Pup mortality at 14 weeks old				
	LM2	MEI_{JS}	2	–5.22
	LM4	$SSTA_{JS}$	2	–4.91
	LM5	$UWI33_{JS}$	2	–4.76
	LM6	$UWI36_{JS}$	2	–4.74
	LM1	PDO_{JS}	2	–4.72
Pup weight at 14 weeks old	PW6	sex+days+$SSTA_{JS}$+sex:days+sex:$SSTA_{JS}$	6	38963.28
Pup weight 14 weeks old and adult female diet	PWD30	sex+days+$SSTA_{JS}$+sex:days+sex:$SSTA_{JS}$	6	20477.06
	PWD13	sex+days+$SSTA_{JS}$+sprich+sex:days+sex:$SSTA_{JS}$	7	20484.25

[1]Model parameter definitions: Year=data collection year, $SSTA_{OJ}$ =Sea Surface Temperature Anomaly between October and June of the following year, $SSTA_{JJ}$ =Sea Surface Temperature Anomaly between June and July, $SSTA_{JS}$ =Sea Surface Temperature Anomaly between June and September, PDO_{JS} =Pacific Decadal Oscillation between June and September, MEI_{OJ} =Multivariate El Niño Southern Oscillation between October and June the following year, MEI_{JS} =Multivariate El Niño Southern Oscillation between June and September, $UWI33_{OJ}$ =Upwelling at 33°N 119°W between October and June of the following year, $UWI33_{JJ}$ =Upwelling at 33°N 119°W between June and July, $UWI33_{JS}$ =Upwelling at 33°N 119°W between June and September, $UWI36_{OJ}$ =Upwelling at 36°N 122°W between October and June of the following year, $UWI36_{JJ}$ =Upwelling at 36°N 122°W between June and July, $UWI36_{JS}$ =Upwelling at 36°N 122°W between June and September, sex=sex of pup, days=number of days from weighing date to 1 October, sprich=species richness of the adult female diet. Model notation: '+' is an additive effect, ':' is a full interaction effect between the variables.

age weight was 17.1 kg for females (SE = 0.60; range 12.6 kg – 20.9 kg) and 19.9 kg for males (SE = 0.60; range 15.3 kg – 23.6 kg); male pups were 2.6 kg (SE = 0.06) heavier than female pups. There was a negative relationship between average $SSTA_{JS}$ and mean pup weights; an increase of 1°C in $SSTA_{JS}$ resulted in 1.0 kg (SE = 0.55) decrease in mean weight of female pups and a 1.4 kg (SE = 0.08) decrease in the average weight of male pups (fig. 2). Average pup weights were the lowest in 1997, 1998, and 2009 when $SSTA_{JS}$ was warmer than normal but in 2011, when $SSTA_{JS}$ was cooler than normal, average pup weights were also low, similar to 1997 and 2009 averages. The inconsistencies in the relationship between $SSTA_{JS}$ and average pup weights indicate that other factors besides oceanographic conditions may contribute to the variability in this parameter.

Adult Female Diet. California sea lions consumed 13 cephalopod taxa and 45 fish taxa (table 5). Pacific hake (*Merluccius productus*), northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), rockfish (*Sebastes* spp.), Pacific saury (*Cololabis saira*), jack mackerel (*Trachurus symmetricus*), California smoothtongue (*Leuroglossus stilbius*), market squid (*Loligo opalescens*), and East Pacific red octopus (*Octopus rubescens*), were the most common prey throughout the time series with FO greater than 10% in at least one of the years.

The first three components of the PCA represented 95% of the variance in the prey composition of the diet. The first component was SSFO of market squid (52% of the variance), the second component was Pacific hake (29% of the variance), and the third component was Pacific sardine (14% of the variance). The PCA identified four diet types: 1) Diet 1 occurred in 2002 and 2005 and had a low SSFO of market squid and a high SSFO of Pacific sardine, 2) Diet 2 occurred in 2000, 2001, 2010, and 2011 and was dominated by market squid and Pacific hake, 3) Diet 3 occurred only in 2003 and was comprised mostly of northern anchovy and Pacific sardine, and 4) Diet 4 occurred in 2009 and was dominated by market squid and rockfish (fig. 3).

Average pup weights tended to be heavier in years represented by Diets 1 and 3, average in years with Diet 2, and the lightest pups occurred in 2009 with Diet 4 (fig. 4). Because diet data were only available for 8 of the 15 years, the best model for pup weights (PW6) was run for the reduced time series and then the AICc was compared to 30 models with diet indices added to determine if adult female diet explained additional variability in pup weights. However, the best model for pup weight

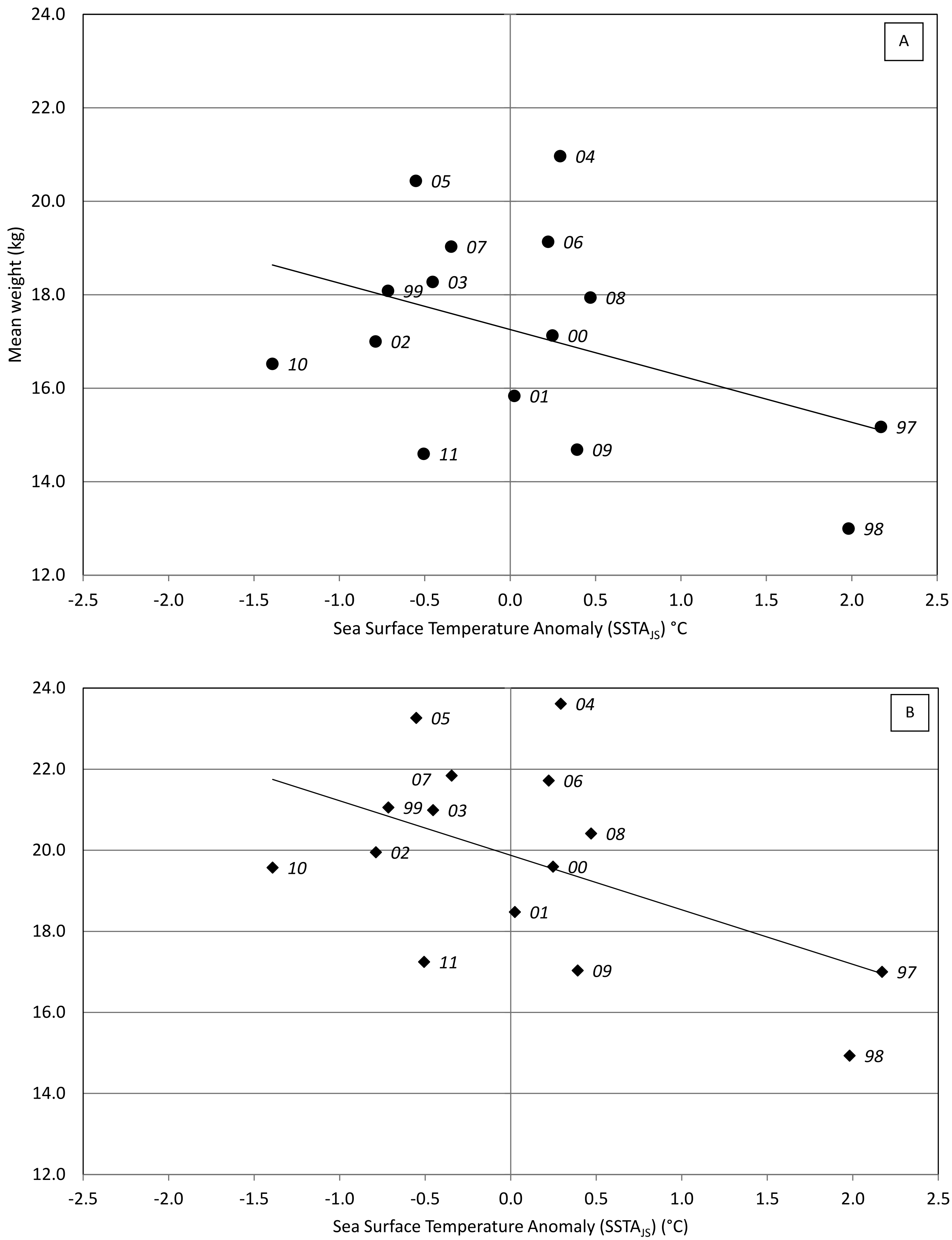

Figure 2. Relationship between the sea surface temperature anomalies ($SSTA_{JS}$) averaged between June and September each year and estimated average mean pup weights of 14-week-old female (A) and male (B) California sea lion pups at San Miguel Island, California.

TABLE 5
Frequency of occurrence (FO) of prey taxons identified from hard parts recovered from fecal samples of adult female California sea lions at San Miguel Island, California. Fecal samples were collected from breeding sites between June and September over 8 years. Taxon code is an abbreviation of the scientific name that was used in Principal Components Analysis (PCA). 'n' is the number of fecal samples collected in each year.

			Year							
			2000	2001	2002	2003	2005	2009	2010	2011
Taxon code	Scientific name	Common name	n = 154	n = 61	n = 98	n = 96	n = 62	n = 64	n = 57	n = 44
Fish										
MERPRO	*Merluccius productus*	Pacific hake	51.3	80.3	42.9	11.5	41.9	15.6	43.9	40.9
ENGMOR	*Engraulis mordax*	Northern anchovy	34.4	23.0	28.6	54.2	37.1	31.3	1.8	0.0
COLSAI	*Cololabis saira*	Pacific saury	24.7	6.6	26.5	13.5	24.2	7.8	0.0	0.0
SEBSPP	*Sebastes* spp.	Rockfish	11.0	13.1	22.4	20.8	16.1	54.7	36.8	18.2
SARSAG	*Sardinops sagax*	Pacific sardine	9.1	1.6	63.3	62.5	61.3	28.1	12.3	6.8
LEUSTI	*Leuroglossus stilbius*	California smoothtongue	5.2	0.0	0.0	0.0	3.2	0.0	15.8	0.0
TRASYM	*Trachurus symmetricus*	Jack mackerel	2.6	9.8	3.1	29.2	12.9	9.4	0.0	0.0
GENLIN	*Genoymemus lineatus*	White croaker	1.9	0.0	0.0	1.0	0.0	0.0	0.0	0.0
SCOJAP	*Scomber japonicus*	Pacific mackerel	1.9	6.6	1.0	1.0	0.0	1.6	0.0	4.5
PEPSIM	*Peprilus simillimus*	Pacific pompano	1.3	1.6	0.0	0.0	0.0	0.0	0.0	0.0
SERPOL	*Seriphus politus*	Queenfish	1.3	1.6	4.1	0.0	0.0	0.0	0.0	0.0
SQUACA	*Squalus acanthias*	Spiny dogfish	1.3	0.0	0.0	1.0	0.0	0.0	0.0	0.0
ATHSTO	*Atheresthes stomias*	Arrowtooth flounder	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CHITAY	*Chilara taylori*	Spotted cuskeel	0.6	0.0	2.0	1.0	0.0	3.1	1.8	0.0
CYMAGG	*Cymatogaster aggregata*	Shiner perch	0.6	0.0	0.0	2.1	0.0	0.0	0.0	0.0
HIPELA	*Hippoglossoides elassodon*	Flathead sole	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LYOEXI	*Lyopsetta exilis*	Slender sole	0.6	1.6	0.0	0.0	0.0	0.0	0.0	0.0
MAGATL	*Magnisudis atlantica*	Duckbill barracudina	0.6	0.0	3.1	0.0	0.0	0.0	3.5	0.0
PORNOT	*Porichthys notatus*	Plainfin midshipmen	0.6	0.0	0.0	0.0	0.0	0.0	3.5	0.0
SEBALT	*Sebastolobus altivelis*	Longspine thornyhead	0.6	0.0	0.0	0.0	0.0	0.0	1.8	0.0
STELEU	*Stenobrachius leucopsarus*	Northern lampfish	0.6	0.0	0.0	1.0	0.0	9.4	1.8	2.3
TARCRE	*Tarletonbeania crenularis*	Blue lanternfish	0.6	3.3	1.0	1.0	0.0	3.1	1.8	0.0
ANOFIM	*Anoplopoma fimbria*	Sablefish	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0
BATPAC	*Bathylagus pacificus*	Pacific blacksmelt	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0
CITSOR	*Citharichthys sordidus*	Pacific sanddab	0.0	0.0	1.0	2.1	0.0	4.7	0.0	0.0
CLUPAL	*Clupea pallasi*	Pacific herring	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
CLUSPP	*Clupeid* spp.	Herring	0.0	1.6	0.0	0.0	1.6	0.0	0.0	0.0
COTSPP	*Cottid* spp.	Sculpin	0.0	0.0	0.0	0.0	0.0	3.1	0.0	0.0
EMBSPP	*Embiotocid* spp.	Surfperch	0.0	0.0	1.0	0.0	0.0	1.6	0.0	0.0
EPTSTO	*Eptatretus stoutii*	Pacific hagfish	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0
GLYZAC	*Girella nigricans*	Opaleye	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0
GOBSPP	*Gobid* spp.	Goby	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0
HEXSPP	*Hexagrammid* spp.	Greenling	0.0	1.6	0.0	1.0	0.0	0.0	0.0	0.0
LEPLEP	*Lepidogobius lepidus*	Bay goby	0.0	0.0	0.0	0.0	0.0	4.7	1.8	0.0
LUMSAG	*Lumpenus sagitta*	Snake prickleback	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3
LYCPAC	*Lycodes pacificus*	Blackbelly eelpout	0.0	0.0	0.0	0.0	0.0	3.1	1.8	2.3
MICPAC	*Microstomus pacificus*	Dover sole	0.0	0.0	1.0	0.0	0.0	3.1	0.0	0.0
MYCSPP	*Myctophid* spp.	Laternfish	0.0	1.6	0.0	1.0	0.0	0.0	0.0	0.0
OSMSPP	*Osmerid* spp.	Smelt	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0
OXYCAL	*Oxyjulis californica*	Senorita	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0
PARSPP	*Paralepid* spp.	Barrcudina	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0
PLESPP	*Pleuronectid* spp.	Righteye flounder	0.0	0.0	0.0	1.0	0.0	0.0	1.8	0.0
PSEMEL	*Psettichthys melanostictus*	Sand sole	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0
STISPP	*Stichaeid* spp.	Prickleback	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0
SYMCAL	*Symbolophorus californiensis*	California laternfish	0.0	3.3	5.1	4.2	3.2	7.8	1.8	0.0
Cephalopods										
LOLOPA	*Loligo opalescens*	Market squid	68.2	83.6	62.2	34.4	37.1	53.1	75.4	47.7
OCTRUB	*Octopus rubescens*	East Pacific red octopus	6.5	0.0	5.1	1.0	8.1	7.8	17.5	20.5
ONYBOR	*Onychoteuthis borealijaponicus*	Boreal clubhook squid	5.2	0.0	6.1	0.0	6.5	6.3	5.3	0.0
GOTSPP	*Gonatopsis* spp.	Armhook squid	3.2	1.6	1.0	0.0	0.0	0.0	0.0	0.0
GONSPP	*Gonatus* spp.	Armhook squid	1.3	1.6	2.0	2.1	0.0	1.6	8.8	2.3
DOSGIG	*Dosidicus gigas*	Humbolt Squid	0.6	0.0	0.0	0.0	0.0	1.6	0.0	0.0
MORROB	*Moroteuthis robusta*	North Pacific giant squid	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ABRFEL	*Abraliopsis felis*	Enope squid	0.0	0.0	1.0	0.0	1.6	1.6	0.0	0.0
GONBER	*Gonatus berryi*	Berry armhook squid	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0
GONBOR	*Gonatopsis borealis*	Boreopacific armhook squid	0.0	0.0	0.0	0.0	0.0	9.4	7.0	4.5
GONONY	*Gonatus onyx*	Clawed armhook squid	0.0	0.0	0.0	0.0	0.0	10.9	19.3	2.3
OCTSPP	*Octopus* spp.	Octopus	0.0	0.0	0.0	0.0	0.0	9.4	0.0	20.5
OMMSPP	*Ommasteuthid* spp.	Flying squid	0.0	0.0	3.1	2.1	0.0	0.0	0.0	0.0

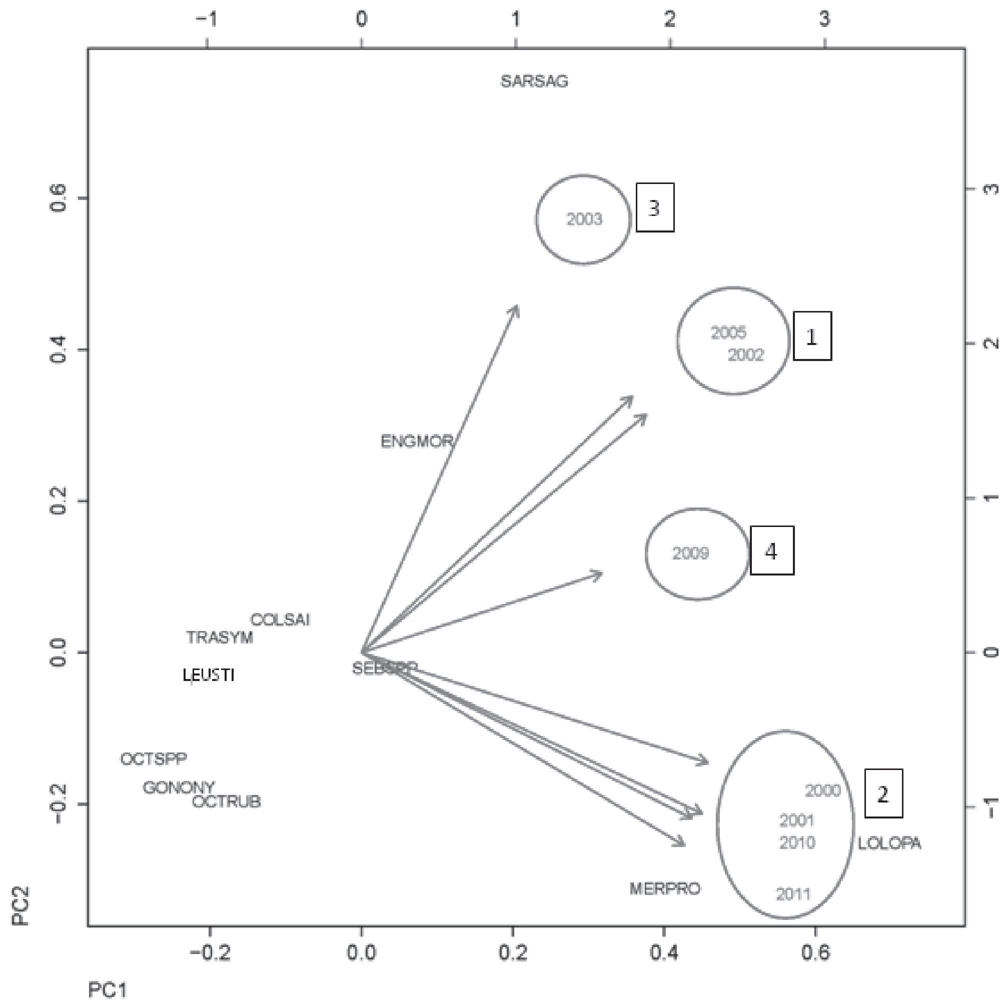

Figure 3. Principal components analysis (PCA) of annual differences of adult female California sea lion prey based on split-sample frequency of occurrence (SSFO) of prey taxa in fecal samples collected at San Miguel Island, California. PC1 represents the annual variation in SSFO of market squid and PC2 represents annual variation in SSFO of Pacific hake relative to other prey taxa in the diet. For clarity, only the prey taxa occurring in SSFO greater than 10% in at least one year are included in the figure but all identified taxa were included in the PCA. Numbers 1–4 indicate unique diet types used in models of pup weights. Taxa codes are listed in Table 5.

during the diet time series (PWD30; table 4) was the same model for the full time series. The best model with diet indices included species richness (sprich) (PWD13; table 4) but was inferior to the model without diet indices included.

DISCUSSION

Reproduction indices of number of pup births and pup mortality at 5 weeks or 14 weeks of age for California sea lions were most sensitive to large scale oceanographic indices, in particular, the MEI. Positive MEI values are associated with El Niño conditions and in years where this occurred, we observed the lowest number of births and highest pup mortality. Negative values of the MEI indicate La Niña conditions and these were generally associated with years of high births but not as consistently as the relationship with El Niño. Variability in the relationships stems from the different characteristics of three ENSO events that occurred during the study (1997–99, 2002–03, and 2009–10). The El Niño phase of these events lasted for several months (Schwing et al. 2006; Bjorkstedt et al. 2011). But the greatest oceanographic changes occurred at different times of the year during each event which resulted in some sea lion population indices being more affected by the events than others (e.g., total births in 1998 vs. 2003). The different impacts of the two phases of ENSO on California sea lion population indices occur because El Niño conditions temporarily reduce the carrying capacity of the CCS and lactating females can only compensate for this with behavioral changes (e.g., longer foraging trips, deeper diving, prey shifting). If the behavioral changes are not sufficient to sustain lactation or gestation, reproductive failure occurs. In contrast, La Niña conditions tend to create a more productive CCS with more abundant sea lion prey and so a greater

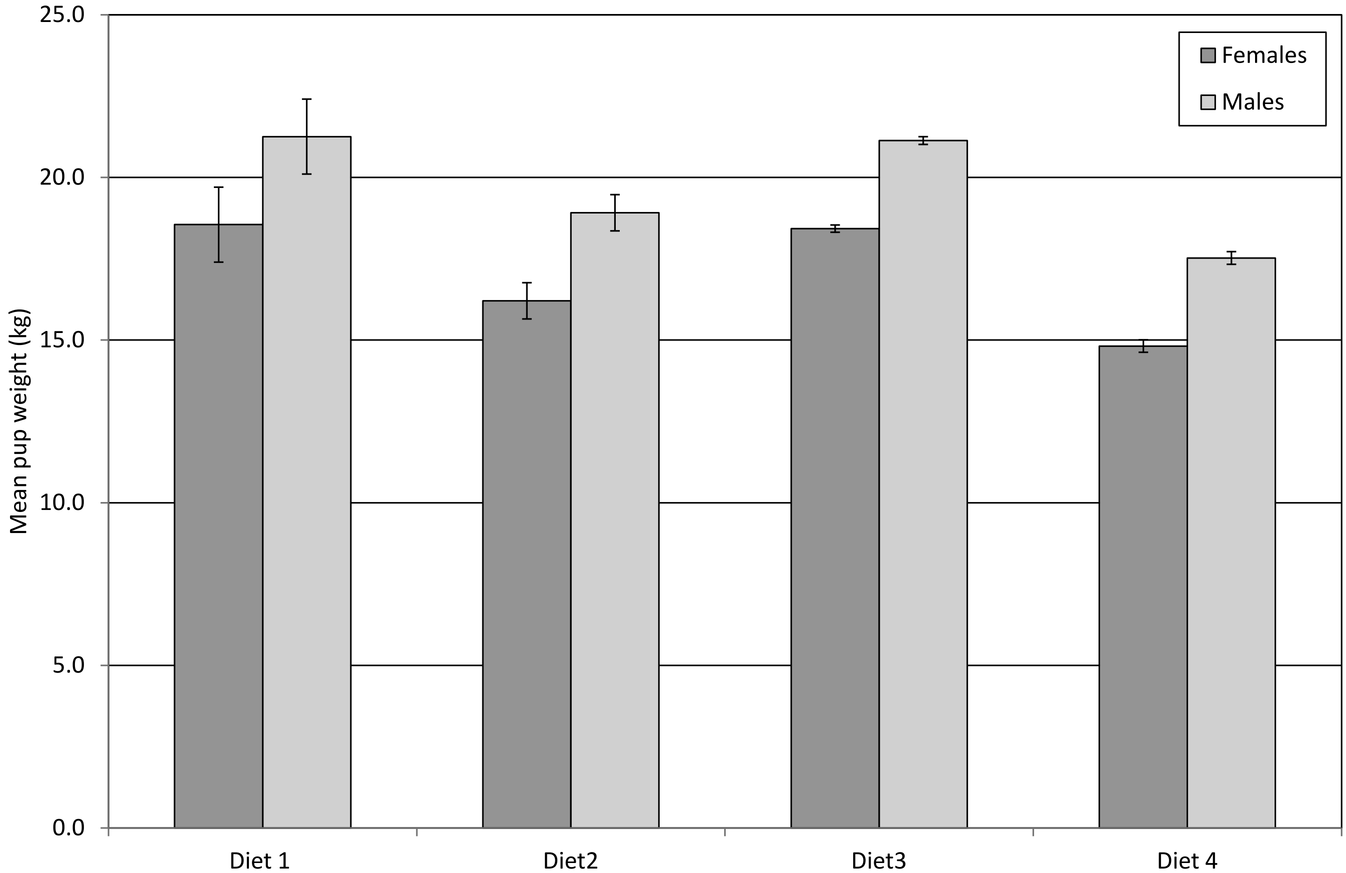

Figure 4. Comparison of four diet types from Principal Components Analysis of adult female California sea lion prey to average weights of 14-week-old California sea lion pups at San Miguel Island, California. Diet 1: high occurrence of Pacific sardine and low occurrence of market squid; Diet 2: high occurrence of market squid and Pacific hake; Diet 3: high occurrence of Pacific sardine and northern anchovy; Diet 4: high occurrence of market squid and rockfish.

number of adult females reproduce and rear their pups successfully.

Small-scale environmental events were also detected by the population indices. Most notably, the sudden collapse of upwelling and productivity as well as elevated sea surface temperatures in the central CCS in May and June 2009 resulted in 74% mortality of 5-week-old pups and highlights the importance of the evolution and timing of local oceanographic events relative to the California sea lion reproductive cycle. The rapid onset of poor foraging conditions at a time when reproductive females were giving birth resulted in high mortality of pups due to starvation (Melin et al. 2010) and failed breeding or pregnancies that contributed to a 41.3% decline in births the following year. Although this event was considered a relaxation event separate from the 2009–10 ENSO, by October 2009 El Niño conditions dominated the CCS (Bjorkstedt et al. 2010). The 2009–10 ENSO was not considered strong compared to historical events (e.g., 1982–84 or 1997–99) and did not follow the normal evolution of these events (Bjorkstedt et al. 2010; Bjorkstedt et al. 2011), but the combination of the relaxation of upwelling in May and June, followed by El Niño conditions from the autumn to spring 2010, had the greatest impact of any event since studies began on the San Miguel California sea lion population in 1972. Thus, the changes in population indices of California sea lions indicated an extreme change in the marine environment that disrupted prey dynamics but that was not interpreted by traditional oceanographic indices until much later. Similarly, in 2004 and 2005, the number of births was lower than average due to localized strong negative upwelling that was not associated with El Niño conditions or regional oceanographic anomalies (Goericke et al. 2005).

Pup weight by 14 weeks of age was perhaps the most sensitive index, responding to relatively small changes in local sea surface temperature with warmer temperatures resulting in lower pup weights. The negative relationship between SSTA and average pup weights was most apparent when SSTs were significantly warmer than normal, 1˚C or greater. Presumably this relationship stems from changes in the availability of sea lion prey to lactating females which results in their inability to fully meet the energetic demands required to nutritionally support their pups. Though we did not find a strong relationship between pup weight and adult female diet, a trend was apparent and a larger data set of diet and pup weight measurements may expose the links between adult female diet, pup growth, and oceanographic indices. Indeed, in Monterey Bay, the diet of California sea lions that were not rearing pups was associated with different ocean conditions (Weise et al. 2006; Weise and Harvey 2008).

Seabird reproductive success has long been considered an indicator of environmental changes because of a relatively direct link between local oceanographic conditions in the CCS, prey availability to adult birds, and success of laying or rearing chicks (Ainley et al. 1995; Abraham and Sydeman 2004; Sydeman et al. 2001; Sydeman et al. 2009). California sea lions range over a greater geographic area of the CCS, measure environmental changes throughout the year, and are sensitive to large and small-scale oceanographic changes, making them an ideal complimentary indicator species for the IEA of the CCS.

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