Temporal variability in ocean climate and California sea lion diet and biomass consumption: implications for fisheries management

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ABSTRACT: Key to understanding ecosystem structure and function in the California Current System is quantitative modeling of trophic interactions of California sea lions *Zalophus californianus*, one of the largest and most abundant predators in this system, and how these interactions are affected by climate variability. Because sea lions consume almost exclusively commercially important prey species, we hypothesized that the potential for competition for specific prey resources would vary with environmental conditions. We evaluated seasonal and annual variation in sea lion diet in Monterey Bay during the strong 1997-98 El Niño and subsequent 1999 La Niña through the examination and identification of prey hard parts found in fecal samples. Annual consumption was modeled using population size, dietary data, sea lion energetics, and prey energy content. Sea lions were plastic specialists, feeding on seasonally abundant aggregating prey, exploiting several species at a time. Short-term seasonal changes in diet corresponded with prey movement and life history patterns, whereas long-term annual changes corresponded with large-scale ocean climate shifts, namely the large 1997-98 El Niño and 1999 La Niña. Annual sea lion consumption of specific prey varied as a function of ocean climate, with an estimated 17 154 t prey consumed in 1998 and 20 229 t in 1999. Sea lion consumption was similar in magnitude to fisheries landings for several prey species and has the potential to adversely impact specific prey resources and directly compete with these fisheries; however, the degree of competition depends on spatial and temporal overlap of fisheries and sea lion foraging efforts.

KEY WORDS: *Zalophus californianus* · El Niño · La Niña · Prey consumption · Bioenergetics model · Trophic interactions · Regime shift

INTRODUCTION

Spatial and temporal variability of physical features in the marine environment affects the distribution and abundance of prey resources (Brodeur et al. 2006), which in turn influences the distribution and behavior of top marine predators (Guinet et al. 2001). Insights into relationships among marine community structure, food webs, and oceanographic features are found by examining characteristics of species at higher trophic levels because they integrate processes at multiple lower trophic levels (Lake et al. 2003). Diet studies of predators are especially informative, because forage species and food webs are commonly affected by physical processes and variability.

In recent years, a number of natural resource agencies have begun integrating principles of ecosystem-based management (EBM) into their organizational philosophy, policy, and structure. Whereas the precise definition of EBM is the subject of great discussion (Browman & Stergion 2004), a key component identified is the quantitative modeling of trophic interactions

that potentially leads to changes in harvest or management strategies (Field et al. 2001). Along the Pacific coast of the United States, recent authorization of the U.S. Magnuson Fishery Conservation and Management Act of 2006, vigorous implementation of the U.S. Endangered Species Act, and enactment of the California Marine Life Management Act of 1998 have placed a new emphasis on restoring the health of coastal ecosystems and fisheries (prey) resources largely through the implementation of EBM. Critical needs for attaining healthy ecosystems are the restoration of over-harvested and/or threatened and endangered fishery populations, identification of essential fish habitats, and the evaluation of the role of predators in marine ecosystems. Increases in some formerly depleted apex predator populations, such as pinnipeds (Costa et al. 2005), that consume commercially important prey species, coupled with development of more intensive fishing methods have increased the potential for competition between pinnipeds and fisheries. However, the dynamics of whether and how this competition may regulate predator and prey populations and affect fisheries and ecosystem structure and health remains unknown.

Trophic connections among marine vertebrates are rarely observed directly. Diets of pinnipeds are frequently inferred from remains of digestion-resistant hard parts of prey in their scats, due to the ease of sample collection and analysis compared to other indirect methods (e.g. stomach lavage, lethal sampling, stable isotopes, and fatty acid signature analyses). Diet studies of pinnipeds have been conducted to understand their role in marine ecosystems and qualitatively and quantitatively assess their impact on fisheries resources (Pierce & Boyle 1991). Bioenergetics models use a combination of population energetic requirements, prey energy density, and diet composition to quantify consumption of prey resources and evaluate the impact of predator consumption on fishery stocks and prey resources (Harvey 1987, Olesiuk 1993).

Waters off central California are part of the California Current System (CCS), a major eastern boundary current and one of the major upwelling regions in the world that varies spatially and temporally (Schwing et al. 1991). Additionally, CCS waters are subject to large-scale, long-term processes associated with the El Niño Southern Oscillation (Lenarz et al. 1995, Lynn et al. 1998). Marine bird and mammal prey species are subject to short-term changes (upwelling) and long-term changes in oceanographic conditions (El Niño) that affect their diet and vertical and horizontal distribution and abundance (Lynn et al. 1998, Brodeur et al. 2006, Soto et al. 2006).

California sea lions are among the most abundant top predators in the CCS, with an estimated 237 000 to 244 000 sea lions in US waters, with annual population increases of 5 to 6.2 % since the passage of the U.S. Marine Mammal Protection Act in 1972 (Carretta et al. 2005). Sea lions consume predominantly commercially important fish species (Lowry et al. 1991, Lowry & Carretta 1999, Weise 2006), and interact and potentially compete with most fisheries along the California coast (NMFS 1997, Weise & Harvey 2005). Whereas the diet of California sea lions off California is well described for southern California (Antonelis et al. 1984, Lowry et al. 1990, 1991, Lowry & Carretta 1999), limited or dated information is available in central and northern California (Ainley et al. 1977, 1982, Bailey & Ainley 1982), and species-specific estimates of prey consumption are not available. Key to understanding trophic interactions within coastal ecosystems and the CCS is insight into the foraging ecology of this large and abundant top predator.

Oceanographic conditions in the CCS shifted dramatically between 1997 and 1999 from El Niño (warm anomalies, low productivity) to La Niña (cool anomalies, high productivity) conditions. The aims of this study were to describe the seasonal and annual variation in diet of California sea lions and to quantitatively model the impact of sea lion consumption on prey and fisheries resources. We predicted there would be dietary differences during the El Niño/La Niña cycle, and our goal was to determine to what extent these changes in the diet and prey-specific consumption estimates were related to anomalous oceanographic conditions in the CCS.

MATERIALS AND METHODS

Sea lion diet. Prey composition and temporal changes in the diet of California sea lions (CSL) in Monterey Bay were determined through identification of prey hard parts found in fecal samples collected weekly from June 1997 through 1999 at sites used exclusively by CSL: Santa Cruz Municipal Wharf (36° 57.5′ N, 122° 1.0′ W) and the United States Coast Guard Jetty in Monterey, California (36° 36.5′ N, 121° 53.4′ W; Fig. 1). Although these sites were inshore, they were representative of CSL diet in central California because there was no significant difference from samples collected from offshore sites (spring 1998; $\chi^2_{0.05,25}$ = 8.04, p = 0.859, M. Weise unpubl. data). Further, average passage rates of prey hard parts from captive CSL (48 h; Orr & Harvey 2001) coupled with average swim speeds for free-ranging animals (2.7 km h^{-1}; Weise 2006) indicated that prey identified in fecal samples were likely consumed throughout the entire central California region (approximately 36° 18.2′ N, 121° 53.7′ W northward to 37° 11.5′ N, 122° 24.3′ W; Fig. 1).
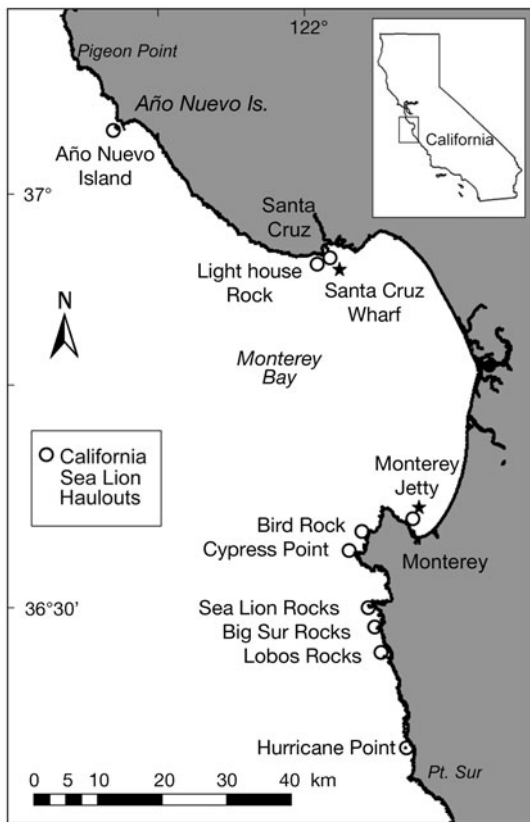
Fig. 1. Location of Monterey Bay along the California coast and California sea lion haul-out sites (○). Fecal sample collections sites (★) and ground census sites were in Monterey and Santa Cruz. Aerial surveys were flown from Pt. Sur to Pigeon Point

Prey hard parts were identified and enumerated using illustrations and pictures (Morrow 1979, Clarke 1986, Cannon 1987, Harvey et al. 2000), a reference collection at University of California Santa Cruz (Weise 2006) and Moss Landing Marine Laboratories (Harvey 1987), and standard protocols for identification of fish bones (Lance et al. 2001). Otoliths and cephalopod beaks were counted, numerical correction factors (NCF) corrected for otoliths lost during digestion (Table 1), and otoliths, beaks, diagnostic salmonid bones, cartilaginous parts and teeth were used to determine a minimum number of individuals (MNI) of each prey species per fecal sample. Prey hard parts were measured, species-specific or an average length correction factor (1.43) were applied (Orr & Harvey 2001), and species-specific linear regressions were used to estimate standard length and mass of fish (Harvey et al. 2000), and mantle length of squid (Wolff 1982). Juvenile-sized spiny dogfish shark *Squalus acanthias* teeth were the only identifiable elasmobranch hard part found in fecal samples with an estimated prey body mass of 500 g.

Contribution of each prey species to seasonal diet was expressed as MNI per species and as a percentage of total estimated mass (%M) of prey ingested, defined as:

$$\%M_{xk} = \frac{m_{xk}}{s_{mk}} \times 100 \qquad (1)$$

where m_{xk} is the mass of prey taxon x during season k, and s_{mk} is the mass of all prey taxa identified during season k.

Diet analysis. Inter-annual and seasonal changes in diet composition were compared and visualized using a non-metric multidimensional scaling (MDS) plot in Primer-E v6.0 (Clarke & Warwick 1994). Plots were based on triangular matrices of Bray-Curtis similarities of percentage biomass contribution of each prey species. Data were not transformed because they provided proportional representation of prey species and weighted dominant taxa. Stress values were calculated to give an indication if and to what extent data were distorted (or scattered). Stress values less than 0.10 were regarded as being unlikely to result in mis-

Table 1. Numerical correction factors (NCF) used to estimate the minimum number of otoliths and cephalopod beaks recovered in California sea lion fecal samples

Prey taxa	NCF	Source
Fishes		
Atherinops californienses	3.7	Orr & Harvey (2001) for *Hypomesus pretiosus*
Chilara talori	1.3	Orr & Harvey (2001) for *M. productus*
Citharichthys sordidus	2.13	Phillips (2005)
Citharichthys stigmaeus	1.07	Phillips (2005)
Clupea pallasi	1.3	Orr & Harvey (2001)
Cymatogaster aggregata	1.7	Bowen (2000)
Engraulis mordax	2.2	Orr & Harvey (2001)
Leptocottus armatus	2.1	Bowen (2000)
Merluccius productus	1.3	Orr & Harvey (2001)
Oncorhynchus spp. (adult size)	0.35[a]	Phillips (2005)
Oncorhynchus spp. (smolt size)	2.7	Orr & Harvey (2001)
Porichthys notatus	1.3	Orr & Harvey (2001) for *M. productus*
Sagax caeruleus	6.87	Phillips (2005)
Scomber japonicus	4.0	Orr & Harvey (2001) for *T. symmetricus*
Sebastes spp.	2.13	Phillips (2005)
Spirinchus thaleichthys	3.7	Orr & Harvey (2001) for *H. pretiosus*
Trachurus symmetricus	4.0	Orr & Harvey (2001)
Cephalopods		
Loligo opalescens	1.1	Orr & Harvey (2001)
Octopus spp.	1.2	Bowen (2000)
[a]Adult salmon pass through an animal in multiple fecal samples, therefore NCF < 1.0		

interpretation of the data (Clarke & Warwick 1994). Seasons were defined as summer (May, June, July), autumn (August, September, October), winter (November, December, January), and spring (February, March, April; Broenkow 1977). Frequency distributions of prey standard length were compared among years using the Kolmogorov-Smirnov (K-S) test in the Systat 11.0 statistical package (SPSS). Cumulative species curves indicated that approximately 31 to 48 fecal samples with hard parts were required to adequately describe diet composition in CSL and compare them among seasons.

To identify environmental variables that best explain temporal variation in sea lion diet composition, the relationships between seasonal percentage biomass of prey species and environmental variables were analyzed using the BIOENV procedure in Primer-E v6.0 (Clarke & Warwick 1994). This procedure iteratively compares the similarity matrices of diet data to environmental data and identifies the subgroup of environmental variables that has a greater weighted Spearman rank correlation (ρ_w). Diet data were used in the Bray-Curtis similarity matrix, and the environmental data matrix used Euclidean distances over log-transformed data.

Variables used as indices of environmental change included sea surface temperature (SST), chlorophyll (chl) *a,* and an upwelling index and their associated anomalies. SST and associated anomalies were created by acquiring 4 km spatial resolution images from the AVHRR Pathfinder equal-angles (V5) dataset (Vazquez et al. 1998) using nighttime passes with a quality flag of 6 or better. These data were spatially projected onto a uniform grid, and temporally binned into monthly composites for 1985 to 2005. Chl *a* and associated anomaly images were created by acquiring nominally 1.1 km spatial resolution images from the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite for 1997 to 2006. Data were spatially projected onto a uniform grid, and temporally binned into 1 d and monthly composites. SST and chl *a* values were integrated over the coastal region where the only study of free-ranging CSL indicated that diving activity was greatest (36° to 39° N and from the coast to 0.5° longitude offshore; Weise et al. 2006), and averaged by month. Anomalies were calculated by subtracting the climatological monthly mean for 1985 to 2005 (SST) and 1997 to 2006 (chl *a*) from the same spatial region. Upwelling indices and anomalies were obtained from the Pacific Fisheries Environmental Laboratory/NOAA website for 36° N 122° W (www.pfeg.noaa.gov). Indices were calculated based upon Ekman's theory of mass transport due to geostrophic wind stress derived from 6-hourly, synoptic, surface atmosphere pressure fields. Monthly

means (±SD) of the daily upwelling indices were calculated.

Bioenergetic model. Annual fish consumption by CSL was estimated using the following bioenergetic prey consumption model based on Harvey (1987):

$$B_{xa} = \sum_{k=1}^{4} [B_{xk} \sum_{t=1}^{3} (N_s \times W_s \times A_s \times E_A \times D_k)] \times (P_{xk}/V_x) \quad (2)$$

Biomass (kg) of prey species x consumed by sea lions during year a (1998 and 1999) was the sum of biomass of prey species x during all 4 seasons k. Biomass of prey species $\times$ during season k was the sum of biomass consumed by sea lion ages t (adult male, sub-adult male/adult female, juvenile) that was a function of the numbers of sea lions present per season (N_s), corrected for the number of individuals at sea based on aerial surveys (W_s), proportion of individuals in each age structure of CSL population for a season (A_s), age-specific daily energetic requirements (MJ d^{-1}) of sea lions (E_A), and number of days in season (D_k) multiplied by the proportion of species x in sea lion diet during season k based on reconstructed biomass of prey species (P_{xk}) divided by energetic density (kJ g^{-1}) of species x (V_x).

Numbers of sea lions (N_s) present were counted each season during monthly aerial photographic surveys in the Monterey Bay region from 1997 to 1999 from Pt. Sur (37° 11.45′ N, 122° 24.26′ W) northward to Pigeon Pt. (36° 18.16′ N, 121° 53.65′ W; Fig. 1). Seasonal counts were corrected for the percentage of individuals at sea (W_s; Lowry & Forney 2005). Age structure of the population (A_s) was the proportion of individuals in each age class counted during biweekly ground surveys from June 1997 to September 1999 in conjunction with fecal collections at the Santa Cruz Wharf (not visible to aircraft) and the jetty in Monterey. Counts from the 2 locations were combined and assumed to be representative of the region.

According to Costa et al. (1991), the total daily energetic requirement (E_A; MJ d^{-1}) for sea lions was determined as:

$$E_A = (E_{A\text{-onshore}} \times \% \text{ time onshore}) + (E_{A\text{-at-sea}} \times \% \text{ time at sea}) \quad (3)$$

where E_A was based on the field metabolic rate (FMR; ml O$_2$ kg^{-1} min^{-1}) measured using doubly-labeled water in lactating adult female CSL (Costa et al. 1991). FMR was integrated over the tagging interval, and data were normalized to estimate at-sea FMR by correcting for the portion of time at sea and onshore. Onshore FMR was assumed to be 2 times an individual's predicted basal metabolic rate (BMR = 61.06 × $M^{0.75}$), and assumed to be similar between years (Costa et al. 1991). FMR for different age classes was scaled to body mass (Weise & Costa 2007; AM: 175 kg,

AF/SAM: 106 kg, Juv: 50 kg); therefore, at-sea FMR was $FMR_{at\ sea} = 304.99 \times M^{0.75}$ and onshore FMR was $FMR_{onshore} = 122.12 \times M^{0.75}$. Field metabolic rates were translated into energetic requirements (E_A) using a conversion factor of 4.8 kcal l^{-1} O_2 and 4.186 J cal^{-1}. Sub-adult and adult males spend 50.3% of their time at sea during a normal year, and 62.5% of their time at sea during a year with anomalously warm ocean temperatures similar to the 1997-98 El Niño (Weise et al. 2006). We assumed that juvenile and adult female CSL in central California spent similar periods of time at sea as sub-adults and adult males. Limited data on juvenile dive behavior or ontogeny of diving in otariids were available; however, our assumption was likely conservative because benthic diving Australian sea lion *Neophoca cinerea* pups and juveniles dove more frequently and spent greater percentage of time at sea diving than adults (Fowler et al. 2006).

Given the lack of detailed energy budgets for otariids, we made simplifying assumptions in calculating the energetic requirements of the CSL population in central California. We did not explicitly account for seasonal variation in energetic requirements associated with reproduction and molt. FMR was scaled to mass with no correction for lactation because no difference in BMR was detected between lactating and non-lactating females (Williams et al. 2007). While the energetic intake of lactating females was greater than non-lactating females (Williams et al. 2007), we assumed the majority of sea lions in the sub-adult male/adult female category were sub-adult males and any females were likely non-lactating given the occurrence of rookeries in southern California.

Proportion of prey species in the diet of CSL each season was estimated using percentage mass (%M) described above. Energetic density (kJ g^{-1}) of prey species (Sidwell 1981, Krzynowek & Murphy 1987, Costa et al. 1991) was multiplied by the metabolizable energy coefficient, which is the amount of usable energy derived per prey species (Costa 1986).

Model error. Estimates of CSL consumption of prey species depend on the precision of data used in the model (sampling error), and the validity of our assumptions where data were unavailable (model error). Two approaches were used to assess uncertainty and sensitivity of input parameters: bootstrapping and a single-parameter sensitivity analysis. Bootstrapping was used to create simulated sampling distributions for each model parameter, and each run of the model randomly selected (with replacement) each parameter from the sampling distributions (Boyd 2002). Parameter distributions were dependent upon the type of data available. Normal distributions were used with data defined by a mean and standard deviation, and uniform distributions were used with data defined by upper and lower limits.

Distributions for each parameter were created using a minimum of 500 iterations because of the estimated standard deviations for all parameters stabilized by this number. Each model run produced a consumption estimate of each prey species for the population of CSL in central California for a given season. Uncertainty estimates (±SD) were determined for 5000 iterations.

Sensitivity analysis was conducted by changing each parameter (S_p) independently by ±1 SD while holding other parameters constant, and then recalculating annual consumption for each prey species, similar to Goldsworthy et al. (2001):

$$S_p = \frac{100(RC'_p - RC_p)}{RC_p} \qquad (4)$$

where RC'_p is the recalculated consumption estimate with parameter p varied by ±1 SD, and RC_p was the consumption estimate of the base model. Simulations were conducted using Matlab 7.2.

RESULTS

Diet composition

Overall, 573 fecal samples (92.2%) contained identifiable prey hard parts with 26 taxa identified to species, an additional 3 to genus, 1 to family, 1 to order, and 1 to class. Of the 16 933 prey occurrences (MNI), 80.6% (13 595) were fishes, and 19.7% (3338) were cephalopods (Table 2). The most numerous fish prey consumed based on MNI were sardines (58.1%), anchovies (8.7%), rockfishes (5.4%), and hake (3.4%; Table 2). Market squid *Loligo opalescens* was the predominant cephalopod prey species (MNI 19.4%), followed by octopus (*Octopus* spp., <0.1%) and other squid (*Gonatus* spp., <0.1%). Based on percentage biomass consumed, schooling pelagic fishes were the predominant fish prey, with sardines *Sardinops sagax* (47.3%) and rockfishes (*Sebastes* spp., 28.6%) the most important prey items, followed by spiny dogfish *Squalus acanthias* (7.8%), market squid (4.7%), jacksmelt *Atherinops californiensis* (2.7%), hake *Merluccius productus* (2.1%), Pacific jack mackerel *Trachurus symmetricus* (2.1%), anchovy *Engraulis mordax* (1.9%), and salmon (*Oncorhynchus* spp., 1.8%; Table 2).

Temporal variation in diet

Seasonal trends as visualized in the MDS plot indicated a state-like shift in CSL diet composition in summer 1998, with the exception of spring 1999 (Fig. 2). Decreasing importance of market squid, variable importance of rockfishes, and increasing importance of

Table 2. Minimum number of individuals (MNI) and percentage mass (%*M*) of prey taxa identified from California sea lion fecal samples collected in Monterey Bay from 1997 to 1999. Indices were derived by applying numerical and size correction factors to otoliths and beaks identified in fecal samples. Number of scats per season with identifiable hard parts in parentheses. Order of species is from the greatest to the least MNI for all seasons combined, and species with total MNI >10 are listed

| | —1997— | 1998 | | | | 1999 | | | |
| | Fall (67) | Winter (70) | Spring (100) | Summer (72) | Fall (68) | Winter (45) | Spring (42) | Summer (32) | Fall (57) |
	MNI %*M*	MNI %*M*	MNI %*M*	MNI %*M*	MNI %*M*	MNI %*M*	MNI %*M*	MNI %*M*	MNI %*M*
Sardinops sagax	144 19.2	522 31.3	976 41.1	2356 64.9	2851 83.2	41 61.8	495 39.0	481 68.6	1979 63.8
Loligo opalescens	384 13.0	1265 10.8	747 5.3	31 0.2	72 0.2	0 0.0	11 0.0	53 2.2	167 1.6
Engraulis mordax	150 3.4	90 2.2	141 1.5	286 2.2	216 1.1	66 0.6	40 0.5	141 5.2	326 2.8
Sebastes spp.[a]	96 27.9	64 39.3	149 18.2	109 17.4	300 5.0	38 11.6	34 38.6	15 3.2	43 3.4
Merluccius productus	69 13.1	10 0.1	95 5.2	40 2.1	96 1.3	35 1.6	44 7.5	62 16.3	118 6.2
Trachurus symmetricus	12 5.4	0 0.0	32 4.0	4 0.6	40 4.1	0 0.0	16 6.2	0 0.0	120 18.6
Citharichthys sordidus	15 1.0	30 1.3	21 1.3	4 0.1	13 0.3	6 0.6	0 0.0	6 2.1	0 0.0
Scomber japonicus	0 0.0	36 9.4	4 1.2	4 1.1	8 0.5	24 11.6	8 5.5	0 0.0	0 0.0
Atherinops californienses	0 0.0	11 0.2	44 10.4	11 1.5	4 0.5	0 0.0	0 0.0	0 0.0	0 0.0
Squalus acanthias	3 3.2	15 3.6	26 5.8	7 1.3	10 1.4	3 11.5	2 2.0	0 0.0	0 0.0
Citharichthys stigmaeus	18 0.7	21 0.1	9 0.1	1 0.0	14 0.1	0 0.0	0 0.0	0 0.0	3 0.0
Cymatogaster aggregata	4 3.1	4 0.4	43 0.3	9 0.1	2 0.0	0 0.0	0 0.0	4 1.9	0 0.0
Octopus spp.	3 0.1	19 0.1	22 0.2	2 0.0	0 0.0	0 0.0	0 0.0	1 0.1	2 0.0
Atherinops affinis	0 0.0	0 0.0	44 0.1	0 0.0	4 0.0	0 0.0	0 0.0	0 0.0	0 0.0
Porichthys notatus	4 1.6	2 0.1	6 0.5	2 0.1	6 0.0	0 0.0	4 0.2	0 0.0	13 1.0
Chilara talori	0 0.0	4 0.1	9 0.2	2 0.0	13 0.1	13 0.0	0 0.0	0 0.0	0 0.0
Clupea pallasi	0 0.0	3 0.1	12 0.8	1 0.0	3 0.0	8 0.1	3 0.6	0 0.0	0 0.0
Leptocottus armatus	5 3.2	0 0.0	4 0.0	0 0.0	0 0.0	4 0.2	0 0.0	0 0.0	0 0.0
Oncorhynchus spp.[b]	2 5.4	0 0.7	2 3.7	5 5.1	1 1.6	0 0.0	0 0.0	0 0.0	2 2.6

[a]Rockfish species were pooled and length and mass regression equations for shortbelly *Sebastes jordani* were used
[b]For adult-sized salmon, skeletal material average mass of gutted salmon landed in the fishery × 1.2 was used (1997: 6.0 kg; 1998: 4.1 kg; 1999: 7.0 kg; PFMC 2000)
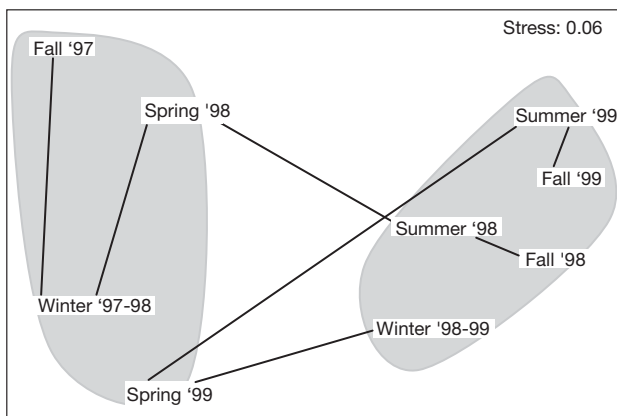

Fig. 2. *Zalophus californianus.* Non-metric, multiple-dimensional scaling (MDS) ordination of California sea lion diet composition based on seasonal Bray-Curtis similarity index of percentage mass of prey consumed in central California from late 1997 through 1999. Shading indicates state-like shift in seasonal diet composition. Maximum stress value was 0.06, and stress levels <0.1 indicate an unlikely misinterpretation of data

sardines in the diet were largely responsible for seasonal trends and state-like shift in diet composition (Fig. 3). Spring 1999 was anomalous with a brief but significant decline in sardines and an increase in rock-

fishes in the diet. There were other notable anomalies in the diet with larger prey species, particularly with greater levels of salmonids in the diet during summer 1998 and fall 1997 and 1999 (Table 2). Also, spiny dogfish were prevalent in the diet in winter and spring, peaking at 11.5% of total biomass consumed in winter 1998-99, and then disappeared from the diet thereafter. Significant differences were apparent in the mean fork length and size distribution of all major prey consumed by CSL between 1998 and 1999 (Fig. 4). Increased hake size was consistent with significantly increased levels of consumption in 1999, whereas increased prey size in 1999 of sardines, squid, and rockfishes was in contrast to decreased occurrence and levels of consumption.

Environment and sea lion diet

Coastal waters off central California were strongly influenced by El Niño conditions beginning in late summer of 1997 and continued into summer of 1998 with decreases in upwelling favorable winds concurrent with greater/higher than normal SSTs (Fig. 3). This was followed by a transition to cool-water La Niña conditions in early 1999 indicated by a sharp increase

in upwelling index that brought cold, nutrient-rich water to the surface (Fig. 3).

Qualitative and quantitative relationships and trends were apparent between environmental variables and seasonal CSL diet composition. Qualitatively, decreasing trends in upwelling and increases in SST in early to
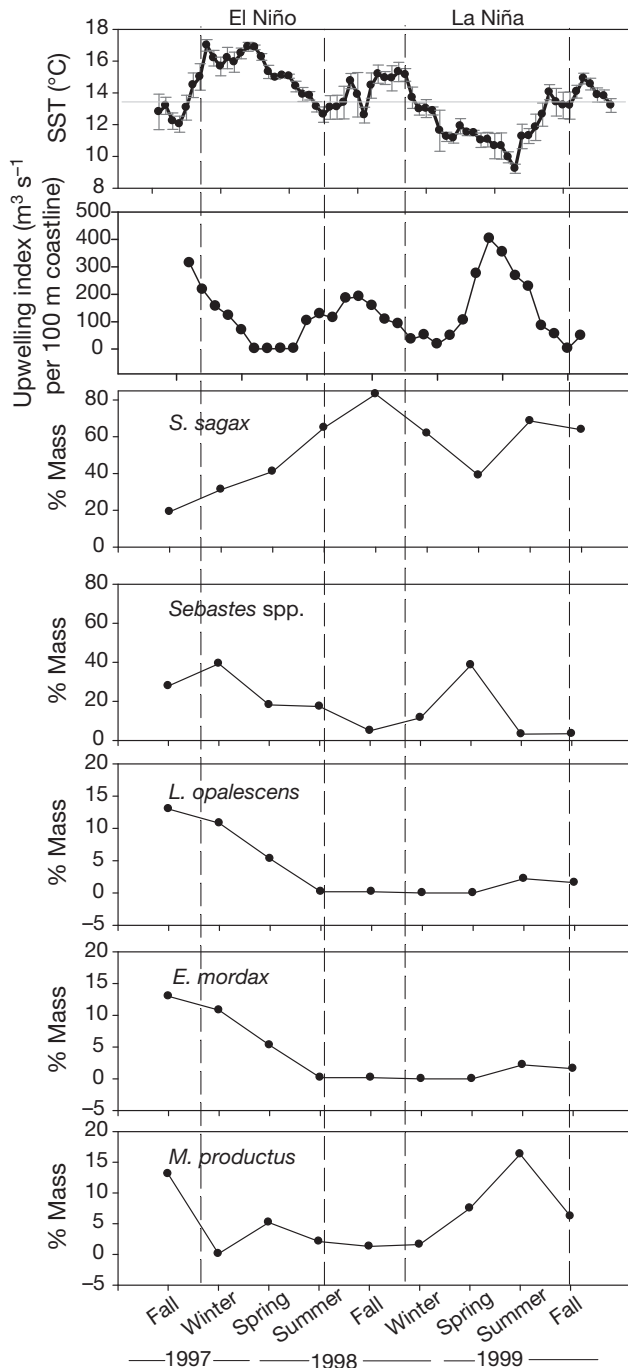

Fig. 3. Oceanographic climatology in central California (mean ± SD) from 1997 to 1999 showing SST (gray line is long-term mean), upwelling index, and the main prey species in the diet of California sea lion based on percentage mass. Vertical dashed lines bound the El Niño and La Niña periods

mid-1998 were concurrent with decreases in the CSL diet of market squid, rockfishes, hake, and anchovy (Fig. 3). During the transition to La Niña conditions in late 1998 and early 1999, however, there were significant and sustained increases in dominance of sardines in the diet, with the exception of spring 1998. As La Niña conditions persisted into summer and fall, sardines, rockfishes, hake, salmonids, and anchovy increased in the diet. Quantitatively, there was a significant correlation between diet composition and environmental conditions. The strongest correlation between CSL diet and environment was indicated by a combination of SST and SST anomaly ($\rho = 0.413$) followed by SST anomaly ($\rho = 0.397$; Table 3).

Population surveys

Monthly aerial surveys (n = 27) indicated that most CSL (mean = 98.4% mo^{-1}, SD = 2.4%) were counted at 8 sites along the central California coast (Table 4). Seasonal trends in abundance of CSL were apparent with greater numbers in late summer and fall (Fig. 5). A significantly greater proportion of CSL in Santa Cruz comprised adult males (mean 83.1%, SD = 11.4%; Kruskal-Wallis, p < 0.001) than sub-adults/females (mean 12.4%, SD = 6.3%) or juveniles (mean 4.4%, SD = 6.2%; Fig. 5). In Monterey, a significantly greater proportion of CSL counted comprised juveniles (mean 74.0%, SD = 18.1%; Kruskal-Wallis, p < 0.001) than sub-adult/females (mean 10.5%, SD = 6.7%) or adult males (mean 14.9%, SD = 15.3%; Fig. 5).

Annual prey consumption

The CSL population in central California (Pt. Sur to Año Nuevo Island) consumed an estimated 17 154 metric tons (t) in 1998 and 20 229 t in 1999 (Table 5). Sardines and rockfishes were consumed in the greatest quantities, and when combined comprised 71.9% of the total biomass consumed in 1998 and 67.3% in 1999. The coefficient of variation varied from less than 0 to 23, and was often greater for species that comprised smaller proportions of the overall diet and/or had greater variability in percentage mass in the diet among seasons.

Because of their greater mass and daily energetic intake, the less numerous adult male CSLs consumed similar proportions (41.5% in 1998 and 44.7% in 1999) of the total biomass as the more numerous juveniles (42.8% in 1998 and 44.9% in 1999) during both years. Less numerous sub-adult males/adult females consumed an estimated 15.7% of the total biomass during 1998 and 10.4% in 1999. Sensitivity analyses indicated that rela-
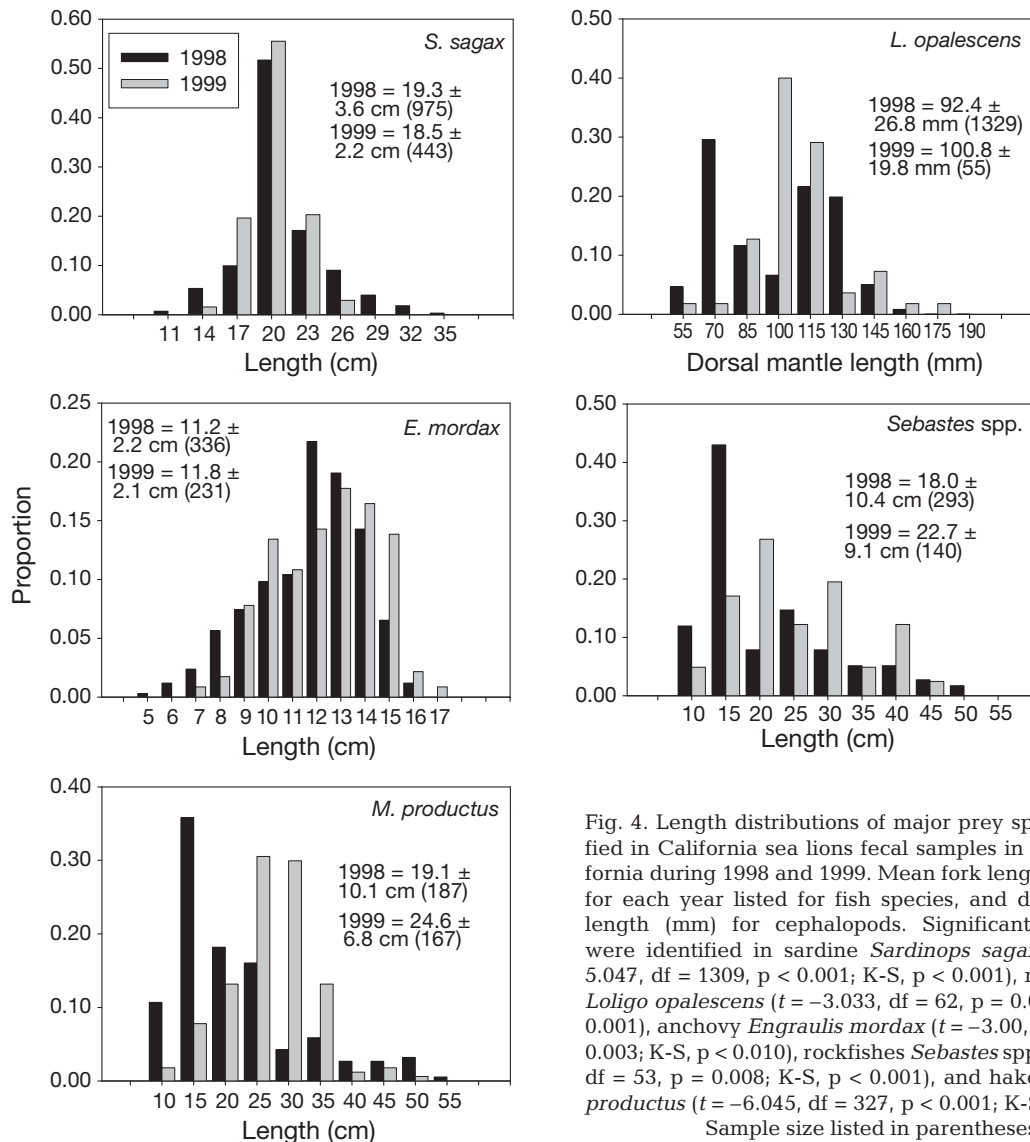
Fig. 4. Length distributions of major prey species identified in California sea lions fecal samples in central California during 1998 and 1999. Mean fork length (±SD, cm) for each year listed for fish species, and dorsal mantle length (mm) for cephalopods. Significant differences were identified in sardine *Sardinops sagax* (*t*-test, $t = 5.047$, df = 1309, p < 0.001; K-S, p < 0.001), market squid *Loligo opalescens* ($t = -3.033$, df = 62, p = 0.004; K-S, p < 0.001), anchovy *Engraulis mordax* ($t = -3.00$, df = 506, p = 0.003; K-S, p < 0.010), rockfishes *Sebastes* spp. ($t = -6.045$, df = 53, p = 0.008; K-S, p < 0.001), and hake *Merluccius productus* ($t = -6.045$, df = 327, p < 0.001; K-S, p < 0.001). Sample size listed in parentheses

tive consumption of CSL was more sensitive to changes in population parameters than metabolic parameters when each variable was varied by ±1 SD% (Table 6). Variability in seasonal population counts and percentage of adult males and juveniles had the greatest impacts on consumption estimates.

DISCUSSION

We found strong seasonal and annual trends in CSL diet resulting from seasonal trends in localized physical forcing (upwelling), prey movements and availability, and annual trends related to ocean climate changes. Significant shifts in ocean climate conditions from 1997-98 El Niño to 1999 La Niña conditions were reflected in CSL diet composition, which shifted from a diet dominated by market squid, anchovy, and rockfishes to predominately smaller sardines, rockfishes, and hake. Although 32 different prey taxa were identified in CSL diet in this study, sea lions were plastic specialists rather than generalists or opportunistic predators because their diet was temporally dynamic, with animals feeding on seasonally abundant schooling or aggregating prey, exploiting several species at a time (Lowry et al. 1991, Orr & Harvey 2001).

Temporal changes in diet and oceanography

During the intense El Niño event of 1997-98, macro-zooplankton abundance during spring 1998 was the lowest recorded in the 50 yr CalCOFI time series, and large changes in the distribution and abundance of

Table 3. BIO-ENV results of the correlation analysis of the relationship between California sea lion seasonal diet composition and environmental factors (SST, SST anomaly, upwelling, upwelling anomaly, chl *a*, chl *a* anomaly). Combinations of environmental factors, *k* at a time, yielding Spearman rank correlation coefficients (ρ) between diet patterns and environmental data. Within each *k* category, parameter combinations are sorted according to their ρ values. **Bold** type indicates the best combination

k	ρ	Best variable combinations			
1	**0.397**	**SST anomaly**			
	0.22	Upwelling			
2	**0.413**	**SST**	**SST anomaly**		
	0.219	SST	Upwelling		
	0.219	SST anomaly	Upwelling		
	0.193	Upwelling	Chl *a* anomaly		
3	0.235	SST	SST anomaly	Upwelling	
	0.226	SST	Upwelling	Chl *a* anomaly	
	0.193	SST anomaly	Upwelling	Chl *a* anomaly	
4	0.226	SST	SST anomaly	Upwelling	Chl *a* anomaly

Table 4. *Zalophus californianus.* Counts of California sea lions on 8 major haul-out sites based on monthly aerial surveys in central California from 1997 to 1999. Common name and location (latitude N/longitude W) are listed for haul-out sites. Total includes only 8 major sites, not other minor sites

Month-Year	Hurricane Point 36°23.84′ 121°54.78′	Lobos Rocks 36°28.31′ 121°56.43′	Big Sur Rocks 36°31.56′ 121°55.97′	Sea Lion Rocks 36°33.2′ 121°56.32′	Bird Rock 36°36.14′ 121°57.94′	Monterey Jetty 36°37.19′ 121°51.32′	Lighthouse Rock 36°56.82′ 122°2.69′	Año Nuevo Island 37°6.65′ 122°20.01′	Total
May 1997	103	68	50	31	0	580	167	2298	3297
June 1997	0	1	0	7	20	50	5	510	593
July 1997	72	351	338	870	706	160	104	2966	5567
August 1997	0	683	32	531	434	39	166	3267	5152
September 1997	62	235	0	155	610	300	195	3039	4596
December 1997	53	481	196	533	1336	849	10	4064	7522
January 1998	73	153	60	424	700	777	73	1958	4218
February 1998	4	18	16	61	261	612	4	2250	3226
March 1998	0	0	0	175	236	330	25	3096	3862
April 1998	52	99	141	672	219	186	48	2831	4248
May 1998	24	131	70	510	255	371	112	2825	4298
June 1998	0	88	0	274	167	171	55	5963	6718
July 1998	0	116	0	237	127	93	49	3252	3874
September 1998	84	91	0	510	351	163	50	5712	6961
May 1999	49	51	0	367	3	113	81	641	1305
June 1999	0	0	165	122	46	22	9	6252	6616
July 1999	269	511	246	358	365	12	11	10883	12655
August 1999	109	152	184	1138	598	221	118	16032	18552
Mean	53	179	83	388	357	281	71	4324	
SD	66	198	103	301	337	260	61	3776	

plankton and pelagic schooling prey species were observed (Lynn et al. 1998). Concurrent with these changes were significant changes in prey size and diet composition (Fig. 3). In addition to shifts in dominant prey species, spiny dogfish and salmonids increased in relative importance during this warmer period (Table 1). These trends in diet were consistent with changes in distribution and abundance of prey species during similar warm water events, particularly northward shifts in schools of adult sardines to central Cali-

fornia (Brodeur et al. 2006), and southward shifts in squid to southern California (Zeidberg 2006). Significant changes in CSL diet composition were recorded during previous El Niño events in southern California (DeLong et al. 1991, Lowry et al. 1991). Consistent with changes in CSL diet during the 1997-98 El Niño, many commercial fisheries reported decreased landings (CalCOFI 1999).

Immediately following the El Niño, a La Niña occurred in late 1998 and persisted throughout 1999. It
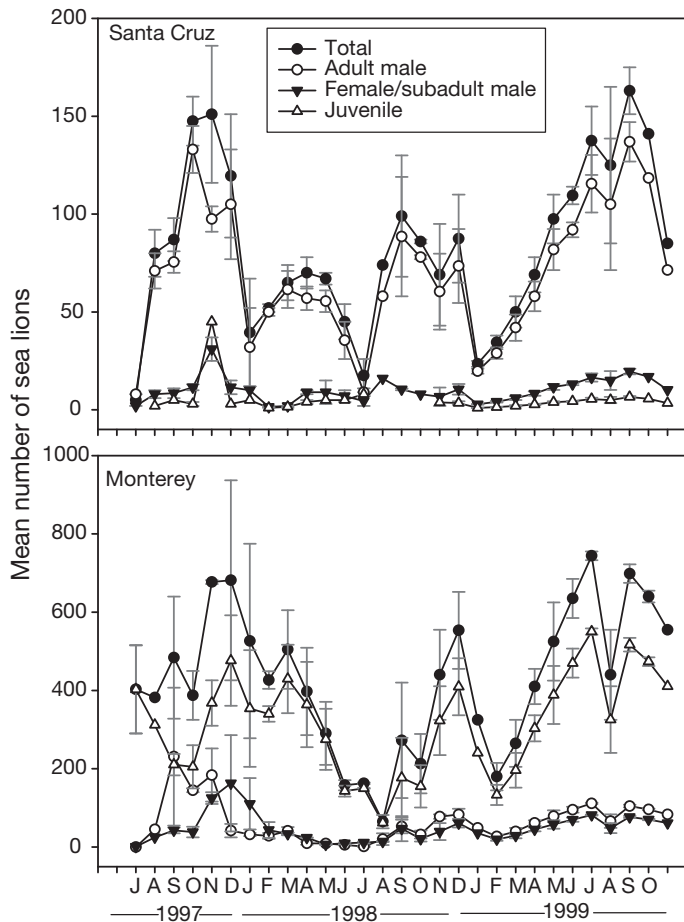
Fig. 5. *Zalophus californianus*. Monthly mean number of adult male, sub-adult male/female, and juvenile California sea lions counted during ground surveys at the wharf in Santa Cruz, California, and the jetty in Monterey, California, from 1997 to 1999. Error bars indicate 1 SE

was characterized by a vigorous offshore-displacement of the California Current, cool near-shore temperatures (Bograd et al. 2000), and a number of population and ecological changes (Schwing et al. 2000). Cool near-shore waters concentrated sardines along the central California coast, which caused the greatest shift in CSL diet characterized by increased dominance of sardines. Also, juvenile rockfishes were farther offshore than in the past, likely because of increased and sustained offshore Ekman transport (Schwing et al. 2000). This corresponded to decreased rockfishes in CSL diet likely due to a lack of availability. A rebound in productivity during 1999 resulted in some of the greatest landings in recent history in market squid and sardine fisheries (CalCOFI 2000), whereas simultaneously, groundfish harvests (flatfishes, rockfishes, and hake) decreased by 37% from 1998. This varied recovery of fisheries likely signifies

spatial heterogeneity in availability of food resources, and likely explains the variability in CSL diet and decrease in prey size during 1999.

Large physical and biological changes during 1998 likely signified the initiation of a new climate regime in the North Pacific (Schwing et al. 2000), and were consistent with the clear and persistent shift in seasonal CSL diet composition from spring to summer 1998 (Fig. 2). A combination of SST and SST anomaly explained the greatest amount of variability in CSL diet composition, which was not surprising given the clear and spatially expansive changes in water temperature (Fig. 3) and its effect on the vertical and horizontal distribution and abundance of pelagically schooling prey species (Lynn et al. 1998). Interestingly, the proposed regime shift in the mid-to-late 1990's was described as going from the warm 'sardine regime' to the cool 'anchovy regime' (Chavez et al. 2003). Our diet data, however, indicated a different type of shift from a warm 'anchovy regime' to a cool 'sardine regime.' This discrepancy was likely due to a difference in spatial scale; Chavez et al. (2003) considered the entire Pacific basin and examined Peruvian fisheries landings, whereas our study focused on CSL diet in the CCS.

Sea lion diet and seasonal prey movements

Although the strong ocean climate signal generated by the 1997-98 El Niño/1999 La Niña clearly impacted CSL diet composition, seasonal and annual movements of prey species and possibly predation risk to CSL also affected diet. For example, older sardines migrated from spawning grounds in southern California and Baja California to feeding grounds in the Pacific Northwest beginning in early summer, whereas younger fish fed off central and northern California year round (PFMC 1999). Seasonal increases of sardines in the diet were consistent with these northward movements, and the size class of sardines consumed by CSL was on the low end of the range of adult fish as predicted for near-shore central California. Market squid occur offshore but prefer shallow, protected near-shore waters to spawn between April and July, with an additional increase between November and January (Fields 1965), which corresponded to increased occurrence of squid in CSL diet during winter 1997-98 and spring 1998. Spawning of most rockfishes increases in winter in central California before the onset of spring upwelling (Love et al. 2002), which was concurrent with seasonal peaks in CSL consumption.

Frequency occurrence and numbers of large prey species in the CSL diet, such as salmon, were relatively low. However, these prey species represented a significant portion of biomass consumed during some sea-

Table 5. *Zalophus californianus*. Estimated annual prey biomass consumption (1000s kg) of California sea lions in central California with standard deviation (SD) and coefficient of variation (CV). Only taxa occurring in the diet during both years were included, and prey hard parts that did not allow for mass estimates were excluded (*Lamtera* spp.). Species listed in order from greatest to least biomass consumed during combined years, 1998 and 1999

Prey species	1998			1999		
	1000s kg	SD	CV	1000s kg	SD	CV
Sardinops sagax	7764.0	3635.5	0.47	9928.6	5524.3	0.56
Sebastes spp.	5255.9	3318.7	0.63	3787.1	4194.9	1.11
Merluccius productus	384.2	804.3	2.09	2018.6	1031.5	0.51
Trachurus symmetricus	371.1	654.7	1.76	1683.2	935.9	0.56
Loligo opalescens	883.7	2127.4	2.41	306.1	2735.5	8.94
Squalus acanthias	414.0	540.7	1.31	667.3	709.0	1.06
Engraulis mordax	334.5	205.6	0.61	584.6	272.9	0.47
Scomber japonicus	311.0	1969.1	6.33	485.4	2519.7	5.19
Oncorhynchus spp.	326.6	209.3	0.64	174.7	281.5	1.61
Atherinops californienses	495.5	140.1	0.28	0.0	199.3	0.00
Citharichthys sordidus	153.6	118.6	0.77	174.4	150.9	0.87
Cymatogaster aggregata	62.1	309.1	4.98	172.7	413.7	2.40
Porichthys notatus	47.4	178.1	3.76	169.5	227.8	1.34
Ophiodon elongatus	200.8	245.8	1.22	0.0	313.8	0.00
Genyonemus lineatus	52.5	33.4	0.64	0.0	52.3	0.00
Lyopsetta exilis	1.0	2.6	2.60	33.5	45.3	1.35
Clupea pallasi	17.9	6.1	0.34	15.3	8.6	0.56
Chilara talori	23.6	8.3	0.35	4.5	12.7	2.82
Citharichthys stigmaeus	14.9	37.9	2.54	2.3	52.9	23.00
Leptocottus armatus	0.8	0.4	0.50	14.8	5.2	0.35
Octopus spp.	8.9	5.6	0.63	4.6	7.4	1.61
Phanarodin furcatus	8.4	2.2	0.26	0.0	3.3	0.00
Symphurus atricauda	7.8	8.0	1.03	0.0	9.8	0.00
Atherinops affinis	6.4	2.1	0.33	0.0	3.4	0.00
Lepidogobius lepidus	3.3	2.1	0.64	0.0	3.5	0.00
Sculpin sp.	1.4	1.7	1.21	1.9	2.0	1.05
Parophrys vetulus	2.1	1.5	0.71	0.0	1.9	0.00
Spirinchus thaleichthys	0.3	0.1	0.33	0.0	0.1	0.00
Other taxa	0.0	0.1	0.00	0.0	0.1	0.00
Total	17153.8			20228.9		

sons or years. The greatest relative importance of salmon in CSL diet was during summer 1998, which coincided with the greatest CSL depredation rates in the commercial and recreational salmon fisheries (Weise & Harvey 2005). Estimated depredation of hooked fish in salmon fisheries accounted for approximately 50.9% of CSL consumption estimates in 1998 and 36.7% in 1999. Therefore, contrary to initial impressions (Weise & Harvey 2005), this implied that CSL were also taking free-swimming salmonids. Synergistic effects of predation risk to CSL and prey availability may affect CSL foraging choices (Frid et al. 2007); however, the lack of data on risk effects to CSL preclude a quantitative analysis or discussion.

Sea lion consumption and fisheries landings

To compare CSL consumption with fisheries landings, annual commercial catch data were obtained from Pacific-Fishery Management Council (PFMC 1999, 2000), and Pacific States Marine Fisheries Commission PacFIN data base (www.psmfc.org/pacificfisheries-information-network-pacfin.html). Sea

Table 6. *Zalophus californianus*. Sensitivity analysis of annual biomass consumption for California sea lions in central California during 1998 and 1999. Percentage change in total biomass consumption estimates when population and metabolic parameters were changed independently ± 1 SD during each year. SD were derived using Monte Carlo simulations (5000 runs) with original data source cited. AM: adult male, AF: adult female, SAM: sub-adult male, Juv: juvenile

Factor	Model parameter	1998		1999		Source
		+1 SD (%)	−1 SD (%)	+1 SD (%)	−1 SD (%)	
Population	Seasonal mean count	22.8	−22.8	46.8	−46.8	This study
	Percentage size class–AM	26.7	−24.1	14.5	−14.5	Weise & Costa (2007)
	Percentage size class–AF/SAM	11.9	−10.9	3.7	−3.7	Weise & Costa (2007)
	Percentage size class–Juv	23.6	−23.4	12.1	−12.1	Weise & Costa (2007)
	% in water correction factor	4.8	−4.8	4.6	−4.6	Lowry & Forney (2005)
Metabolic	Body Mass–AM	7.5	−8.0	8.1	−8.6	Weise & Costa (2007)
	Body Mass–AF/SAM	2.5	−2.7	1.7	−1.8	Weise & Costa (2007)
	Body Mass–Juv	12.1	−13.4	12.7	−14.1	Weise & Costa (2007)
	Daily energy required–AM	5.7	−5.7	6.2	−6.2	Costa et al. (1991)[a]
	Daily energy required–AF/SAM	2.2	−2.2	1.4	−1.4	Costa et al. (1991)[a]
	Daily energy required–Juv	5.9	−5.9	6.2	−6.2	Costa et al. (1991)[a]
	% time at sea /% time onshore	9.1	−9.1	7.6	2.3	Weise et al. (2006)
	Metabolic efficiency (prey items)	−2.3	2.3	−2.2	2.3	Costa (1986)

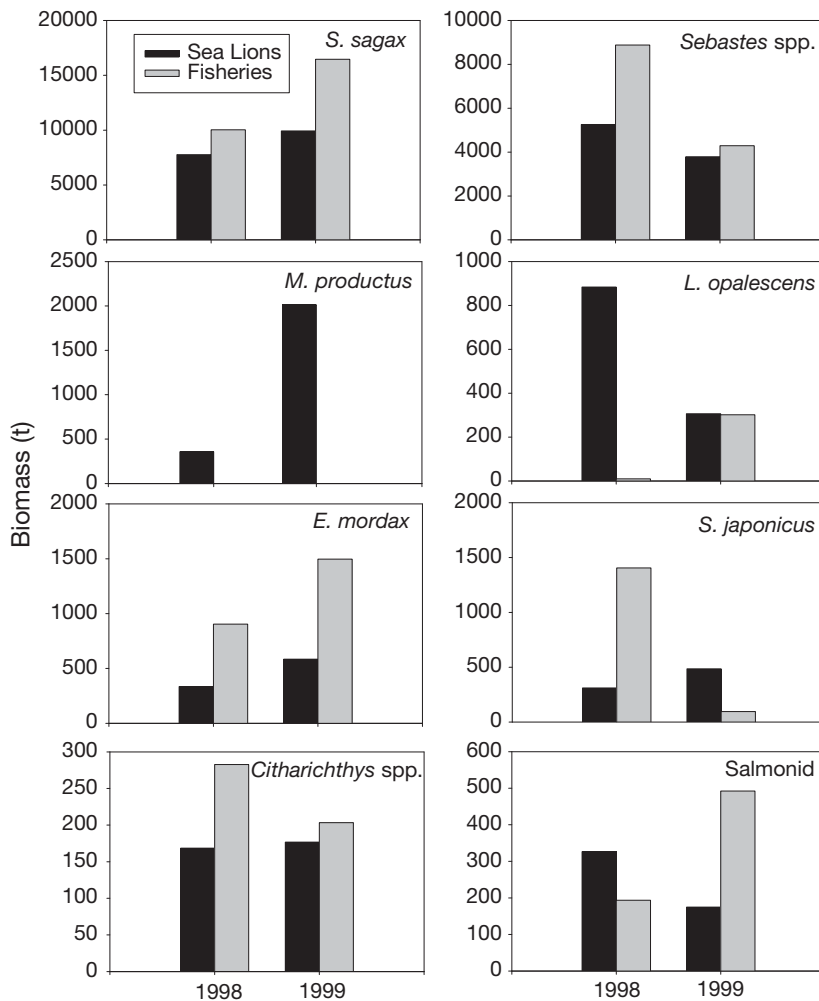[a]Scaled to mass based on 1 ± SD from adult female (Costa et al. 1991)

Fig. 6. *Zalophus californianus.* Comparison of estimated annual prey consumption (in 1000s kg) of California sea lions in the Monterey Bay region and commercial fisheries landings (in 1000s kg) for 1998 and 1999. Comparisons were limited to species important to fisheries and availability of data. See Table 5 for full species names

fishes, 37 to 39% of anchovy, and 60 to 87% of sanddab fishery landings (*Citharichthys* spp.; Fig. 6). Although hake is one of the largest fisheries on the west coast of North American, there were few landings in central California.

Consistent trends in CSL consumption and fisheries landings were likely due to similarities in prey availability, whereas differing trends were likely multifactorial. For example, fishers reported in 1998 that squid were unavailable; however, CSL consumed an estimated 884 t or just less than 5% of their total consumption. Squid were available to sea lions, but were likely offshore and beyond the depth range of the squid fleet, whereas during La Niña conditions, squid were available inshore and landings resumed; however, percentage mass and total consumption estimates declined in CSL diet possibly due to availability of more profitable prey (sardine, rockfishes, and hake). While increased salmon in CSL diet during 1998 was consistent with increased depredation rates in fisheries (Weise & Harvey 2005), decreased CSL consumption in 1999 may reflect the availability of preferred prey and/or difficulty in handling salmonids that approximately doubled in body size (PFMC 2000).

Sea lion impacts on fisheries and marine resources

To evaluate the potential for competition with fisheries, prey-specific estimates of CSL biomass consumption were evaluated in the context of fish stock estimates. Although many stock assessments often were on a much larger spatial scale than central California or were non-existent, this initial comparison to CSL consumption estimates enabled us to identify stocks where competition was more likely and highlighted research needs.

Our study region was approximately 9% of the California coast (based on linear distance), and for simplicity, we assumed that fish stocks were equally distributed along the coast. The most recent stock assessment for sardines in California reported 1.07 million t in 1998 (including data from Mexico and the U.S.; Hill et al. 2002); therefore, the sardine stock in central California was approximately 96 300 t. Annual consumption of sardines by CSL in 1998 represented approximately 8.1% of the total stock in central California and 10.3%

lion consumption was greater in 1999 (20 228.9 t) than in 1998 (17 153.8 t), which was likely due to greater numbers of animals present in central California during La Niña conditions in 1999. Because of the virtual collapse of many commercial fisheries during the 1997-98 El Niño, CSL consumed a significantly greater equivalent proportion of commercial landings than during 1999 (Fig. 6). Conversely, because of record commercial landings of several important prey taxa during 1999, equivalent percentages of commercial landings consumed by CSL were lower. CSL consumption exceeded commercial fisheries landings for market squid and salmonids in 1998 and mackerel (*Trachurus symmetricus* and *Scomber japonicus* combined) and market squid in 1999 (Fig. 6). Otherwise, CSL consumed the equivalent of 60 to 77% of sardine fishery landings, 59 to 84% of rock-

in 1999. Mackerel biomass (*Trachurus symmetricus* and *Scomber japonicus*) was 104 320 t in 1998 and 60 491 t in 1999 (Hill et al. 2002), and anchovy biomass was 432 000 t in 1994 (Jacobson et al. 1994); therefore, CSL consumed approximately 13.8 to 39.8 % of mackerel biomass and 0.9 to 1.5 % of the anchovy biomass. Coastal hake stock was 1.67 million t in 1998 (Dorn et al. 1999), so CSL in central California consumed 0.02 % to 0.12 % of that stock in 1998 to 1999. Evaluating sea lion impacts on some key prey assemblages was problematic, as stock assessments were not available for market squid or sanddabs and only some species of rockfishes, which were not identified to species in CSL diet.

The best estimate of numbers of Chinook salmon passing through Monterey Bay was the California Central Valley Index (CVI; 1998: 611 800 fish; 1999: 636 500 fish; PFMC 1999, 2000), which was a combination of ocean and inland harvest plus escapement estimates for all races of Central Valley Chinook. Assuming that the average mass of salmon landed in the commercial fishery (1998: 4.1 kg; 1999: 7.3 kg, adding 20 % to compensate for gutted mass) represented the average mass of CVI Chinook and fish consumed by CSL, 13.0 % of the total Chinook salmon biomass available in central California was consumed during 1998 and 3.8 % in 1999.

Although the potential competition between CSL and fisheries varied annually in a prey-specific mode with ocean climate, our analysis indicated that CSL consumption of mackerels, salmonids, sardines, and possibly rockfishes could adversely impact prey resources and directly compete with these fisheries depending on the year. Foraging by apex predators can initiate forces that cascade across successively lower trophic levels, and at times, have the potential to restructure trophic complexity through changes in the number and/or strength of interactions among trophic levels (Estes et al. 1998). This is of concern for certain CSL prey species, particularly when CSL consumption is coupled with fisheries harvests. Conversely, these prey species may regulate the CSL population, depending on ocean climate (i.e. El Niño), and assuming that the CSL carrying capacity is food imited.

The importance of rockfishes in CSL diet would benefit from further investigation because otoliths were not identified to species. While it was likely that rockfish prey were common and abundant noncommercial species, such as shortbellies *Sebastes jordani*, there was potential for competition and impact on this prey resource even if a small percentage of rockfishes consumed were listed species, such as Bocaccio rockfish *S. paucispinis*. Other prey species (hake, anchovy, market squid, sanddabs) were prevalent in the diet and comparable to fisheries landings in quantity; however,

these species were likely not regulating the sea lion population, and sea lions were not directly competing with fisheries because of greater standing stock biomass. Although CSL consumption may have been in direct competition with some fisheries, prey resources may have been particularly impacted on a spatially explicit basis if CSL and fisheries were removing fish simultaneously in the same area. Further investigation is needed to identify the spatially-explicit foraging areas of CSL compared to geo-referenced catch per unit effort of key fisheries in the CCS.

Spatial interpretation of our analysis was limited to central California because of the variability in prey abundance and distributions, and sea lion diet and occurrence along the west coast. However, this study highlighted the need to assess the potential for competition between fisheries and sea lions in other population centers, including the Farallon Islands and major rookery sites in southern California. An obvious question was whether CSL consumed similar-sized fish as those landed in fisheries, but lack of availability of such fisheries data limited this comparison.

Data limitations

Traditionally, competition between pinnipeds and fisheries, and pinniped food habits have been evaluated through the visual analysis of fish sagittal otoliths and cephalopod beaks found in gut contents or fecal samples of pinnipeds (Harvey 1987, Cottrell et al. 1996). Because otoliths can be partially or totally digested as they pass through the gut of seals (Dellinger & Trillmich 1988, Harvey 1989, Bowen 2000) size and frequency of prey can be underestimated (Dellinger & Trillmich 1988, Harvey 1989, Cottrell et al. 1996, Bowen 2000, Orr & Harvey 2001). When prey structures in addition to otoliths were identified in fecal samples, frequency and number of individual prey were at least 2 times greater for many prey taxa (Olesiuk 1993, Cottrell et al. 1996, Lance et al. 2001, Browne et al. 2002). Cartilaginous fishes may be underestimated in the diet if their statoconia were completely digested before excretion (Everitt & Gearin 1981). Estimates of diet in this study were therefore determined using numerous prey hard parts.

Estimation of prey length and weight of prey species consumed by CSL was difficult because of natural variability in otolith length to prey length relationships, and because the degree of otolith erosion during digestion was affected by meal size, activity level, size of prey, and physical structure of prey hard parts (Dellinger & Trillmich 1988, Harvey 1989, Cottrell et al. 1996). Identifying all salmonid hard parts and centra and teeth of cartilaginous fishes in fecal samples

addressed potential biases that might underestimate salmon and cartilaginous fishes in the diet. Use of non-specific correction factors compensated for otolith degradation during digestion, and numerical correction factors compensated for otolith loss during digestion. Therefore, conclusions regarding the relative importance and proportions of prey species in CSL diet were likely robust.

As with previous studies that estimated biomass consumption of pinnipeds, there were inherent sources of error and variability, and numerous assumptions that must be considered when interpreting the results. The importance of each parameter in our model was evaluated using the sensitivity analysis, regardless of the source of variability or assumptions. This approach highlights parameters of greatest interest in refining estimates of CSL consumption in central California, and can serve to direct future research efforts. Sensitivity analysis indicated that the precision of the seasonal number of CSL and the proportion of individuals in different age classes were the primary parameters affecting consumption estimates. Although complications introduced by migrating individuals and varying presence of different age classes of sea lions were identified as complications in a report by NMFS (1997), our results quantify this sensitivity and highlight the need for refined census methods and research in these areas.

CONCLUSIONS

This study provides the most detailed analysis of CSL diet in central California, and some of the first quantitative evidence that CSL diet was directly affected by ocean climate changes. Further, we documented the impact of ocean basin-level regime shifts on a top predator diet with a significant and relatively stable change in diet from a warm 'anchovy regime' to a cool 'sardine regime.' CSL had a diverse diet, as evidenced by the 32 prey taxa identified in this study and others (Lowry et al. 1990, 1991, Lowry & Carretta 1999); however, it was clear that they were plastic specialists concentrating their efforts on a handful of prey species in each season and switching prey with ocean climate shifts and seasonal movement of prey. Despite inherent biases and necessary assumptions in biomass consumption models, some of which are not testable or are not easily testable, our model provided an initial quantitative measure of trophic interactions in the CCS. Further, this model enabled the evaluation of the potential for competition between CSL and fisheries, and impacts on ecosystem structure and function. Although limitations on the availability of data or inherent error in data (sampling or model) will lead to errors in con-

sumption estimates, we believe that the strong trophic linkages identified between CSL and specific prey species that are of commercial importance are unlikely to change. As more data on bioenergetic model parameters and prey species stock assessments accumulate, the uncertainties will be reduced. This bioenergetic model provides key data, and a food-web modeling framework that can be used to model trophic interactions with other predators, which are essential to the goals and implementation of EBM in the CCS.

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