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Food habits of Steller sea lions (*Eumetopias jubatus*) off Oregon and northern California, 1986–2007

Susan D. Riemer[1] **(contact author)**
Bryan E. Wright[2]
Robin F. Brown[2]

Email address for contact author: susan.d.riemer@state.or.us

[1] Oregon Department of Fish and Wildlife
Marine Mammal Research Program
1495 E. Gregory Road
Central Point, Oregon 97502

[2] Oregon Department of Fish and Wildlife
Marine Mammal Research Program
7118 NE Vandenberg Avenue
Corvallis, Oregon 97330

Abstract—We described the diet of the eastern stock of Steller sea lions (*Eumetopias jubatus*) from 1416 scat samples collected from five sites in Oregon and northern California from 1986 through 2007. A total of 47 prey types from 30 families were identified. The most common prey was Pacific hake (*Merluccius productus*), followed by salmonids (*Oncorhynchus* spp.), skates (Rajidae), Pacific lamprey (*Lampetra tridentata*), herrings (Clupeidae), rockfish (*Sebastes* spp.), and northern anchovy (*Engraulis mordax*). Steller sea lion diet composition varied seasonally, annually, and spatially. Hake and salmonids were the most commonly identified prey in scats collected during the summer (breeding season), whereas hake and skate were most common in the nonbreeding season. Continued research on Steller sea lion diet and foraging behavior in the southern extent of their range is necessary to address issues such as climate change, interaction with competing California sea lions, and predation impacts on valuable or sensitive fish stocks.

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Knowledge of an animal's diet is important for understanding its foraging behavior, habitat use, and population dynamics, and this knowledge is of particular importance when considering threatened and endangered species. Steller sea lions (*Eumetopias jubatus*) are a case in point. Ranging throughout the North Pacific Rim from California to Japan (Loughlin et al., 1984; Pitcher et al., 2007), Steller sea lion populations in western Alaska underwent dramatic declines from the late 1970s to early 1990s (Braham et al., 1980; Merrick et al., 1987; Loughlin et al., 1992; Trites and Larkin, 1996). This population was listed as "threatened" under the Endangered Species Act (ESA) in 1990, and later the western stock was listed as "endangered" (Loughlin, 1997; NMFS, 2008). The primary hypothesis for the decline has been chronic nutritional stress related to changes in diet (Springer, 1992; Merrick and Loughlin, 1997; Trites and Donnelly, 2003; NMFS, 2008).

With the nutritional stress hypothesis (Springer, 1992; Merrick et al., 1997; Trites and Donnelly, 2003), and its successor, the ocean climate hypothesis (Trites et al., 2007a), declines in the Steller sea lion western distinct population segment (WDPS) were proposed to be the result of changes in the quantity, quality, and availability of prey, brought about by an ocean climate regime shift in 1976–77 (but see Fritz and Hinckley, [2005]). This shift is hypothesized to have forced Steller sea lions to change their diet and to have resulted in chronic nutritional stress manifested by reductions in body size, productivity, and juvenile and pup survival (York, 1994; Trites and Donnelly, 2003). Other explanations for the decline of the WDPS that were considered but rejected included population redistribution, commercial and subsistence harvest, predation, pollution, and entanglement in marine debris (Merrick et al., 1987).

Although the Steller sea lion WDPS experienced annual declines in abundance ranging between 1.6% and 5.2% (Merrick et al., 1987), the abundance in the eastern distinct population segment (EDPS) increased at 3.1% per year from 1977 through 2002 (Pitcher et al., 2007; NMFS, 2008). The hypothesized role of poor diet in the decline of the WDPS, contrasted with the increasing EDPS, begs the question as to what type of prey the Steller sea lion EDPS consumes and how does it compare with that of the WDPS. The majority of information on Steller sea lion diet, however, has come from Alaska (e.g., Pitcher, 1981; Merrick et al., 1997; Sinclair and Zeppelin, 2002; Womble and Sigler, 2006; Trites et al., 2007b; McKenzie and Wynne, 2008). In this

study, we provide data on Steller sea lion diet from the southern extent of the EDPS range based on 1416 scat (fecal samples) collected from five sites in Oregon and northern California from 1986 through 2007. We tested for seasonal, annual, and spatial differences in diet composition and discuss our results in relation to findings from Alaska.

Materials and methods

Field and laboratory

We collected scat from four locations off Oregon and one location off northern California from 1986 through 2007 (Fig. 1; Table 1). Three of the five locations were occupied seasonally as rookeries (Orford Reef, Rogue Reef, St. George Reef), whereas the other two were strictly nonbreeding haul-outs (Columbia River South Jetty, Cascade Head). Scats collected from May through August were classified samples from the "breeding season" and scats from the remainder of the year, as samples from the "nonbreeding season." Scats were collected opportunistically as part of other research activities or during dedicated food habit collection trips.

Scat samples were collected and processed according to the method described in Lance et al.[1] Collections made after 2003 were processed with a standard washing machine according to collection and processing procedures described in Orr et al. (2003). Recovered hard parts were examined with a dissecting microscope and identified to the lowest possible taxonomic level by comparing all identifiable prey remains (e.g., bones, otoliths, cartilaginous parts, lenses, teeth, and cephalopod beaks) with a comparative reference collection of fish from the northeastern Pacific Ocean and Oregon estuaries. Individual samples that contained both identified prey and remains too eroded to be identified (unidentified fish) were included in this analysis, whereas samples with only unidentified remains (n=11) or no remains (n=22) were not.

Data analysis

We summarized the relative importance of prey in sea lion diet by calculating the frequency of occurrence (FO) of each prey type. Frequency of occurrence was defined as the number of scat containing a given prey type divided by the number of scat with identifiable prey. Although other summary statistics are possible, FO is a simple calculation, widely used, and probably least affected by differences in prey recovery (Tollit et al., 2010). We calculated exact 95% confidence intervals

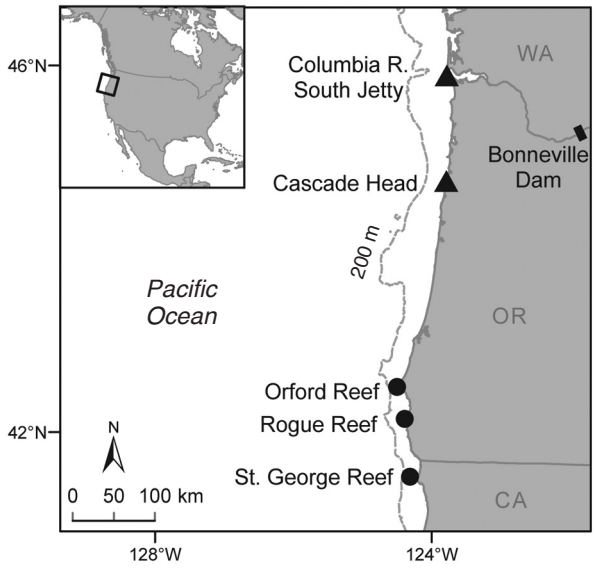

Figure 1

Locations (solid circles=rookeries, solid triangles=haul-outs) where Steller sea lion (*Eumetopias jubatus*) scat was collected off Oregon and northern California, 1986–2007. See Table 2 for detailed information on sampling locations and effort.

for FO by assuming that the number of scat in a collection containing a given prey was binomially distributed.

In addition to univariate summaries, we were also interested in testing whether multivariate diet composition differed between collections. Wright (2010) and Lemons et al. (2010) noted that the common practice of using chi-square tests to compare diets violates the assumption of independence for that test by ignoring the nesting of multiple prey items within a scat. Violation of the assumption of independence results in psuedoreplication and biased chi-square statistics. More appropriate alternatives for comparing multivariate diet composition between groups include distance-based permutation methods (e.g., Luo and Fox, 1996; Anderson, 2001; Berry and Mielke, 2003); multiple-response categorical variable methods (e.g., Agresti and Liu, 1999; Bilder and Loughlin, 2009; Nandram et al., 2009); and mark-recapture methods (Lemons et al., 2010). We chose the distance-based Mantel test (Mantel, 1967; Luo and Fox, 1996) because it could be formulated to address our questions of interest, was easy to implement in existing software, and has been used by other researchers studying animal diets (e.g., Hudon and Lamarche, 1989; Green and Burton, 1993; Jones and Barmuta, 1998).

We implemented Mantel tests, using package "vegan" (Oksanen et al., 2009) in R (R Development Core Team, 2009). We tested whether diet composition differed by month (after controlling for year and site), year (after controlling for month and site), or site (after controlling for month and year). Distances among scat samples were computed using the Jaccard coefficient which is an asymmetrical binary coefficient commonly used to compare sampling units using species presence-absence

[1] Lance, M. M., A. J. Orr, S. D. Riemer, M. J. Weise, and J. L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. AFSC (Alaska Fisheries Science Center) Proc. Rep. 2001-04, 36 p. Alaska Fisheries Science Center, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

Table 1

Total number of Steller sea lion (*Eumetopias jubatus*) scat collected by site, month, and year from haul-outs and rookeries in northern California and Oregon, 1986–2007.

		Breeding season month				Nonbreeding season month								
Location	Year	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Total
Columbia River[1]	2004		55		38	45							51	189
	2006				48									48
	2007			20	61	3								84
Cascade Head[2]	2003							13		11				24
Orford Reef[3]	1990			41										41
	2002			15										15
Rogue Reef[4]	1986		18											18
	1987		40											40
	1988		20											20
	1990			47										47
	1993		36											36
	1994		33											33
	1995		12											12
	1996	60												60
	2001		70		48								46	164
	2002			33	37							42	78	190
	2003			12				54					57	123
	2004			33										33
	2005	2		13									20	35
	2006			25										25
St. George Reef[5]	1990			4										4
	1994		37											37
	2002			35										35
	2003			29									7	36
	2004			34										34
	2006			33										33
Total		62	321	374	232	48	67	0	0	11	0	42	259	1416

[1] South Jetty (46.233 lat. N, 124.070 long. W).

[2] Sea Lion Cove (45.067 lat. N, 124.013 long. W).

[3] Long Brown Rock (42.791 lat. N, 124.605 long. W).

[4] Primarily Pyramid Rock (42.444 lat. N, 124.469 long. W), but also surrounding sites including Needle Rock (42.448 lat. N, 124.483 long. W), Double Rock (42.449 lat. N, 124.490 long. W), and South Seal Rock (42.436 lat. N, 124.465 long. W).

[5] South Seal Rock (41.813 lat. N, 124.351 long. W).

data (Legendre and Legendre, 1998). A Jaccard distance of zero indicates that two scat shared all of the same prey items, whereas a distance of one indicates that they had no prey items in common. We paired the Jaccard distance matrix with a design matrix consisting of zeros for between-population distances and $1/(n_i-1)$ for within-population distances (where i indicates population membership; see Manly, 1997). When used with a design matrix the Mantel test is equivalent to a nonparametric multivariate analysis of variance (Sokal and Rohlf, 1995).

We compared diets based on prey identified to the lowest possible taxon in order to limit the potential for spurious differences arising from an arbitrary categorization of prey types, although this procedure resulted in some comparisons where data were not at an equivalent taxonomic level. Analysis based on additional categorization of prey—such as size, ecology, or abundance—although potentially useful, was beyond the limits of what the data could support. We restricted statistical comparisons to selected unpooled collections with at least 30 samples. For each test, 9999 randomizations were used to obtain the distribution for the Mantel test statistic (r_M) and to calculate probability (P) values. A significance level of $\alpha=0.002$ was used based on a Bonferroni adjustment of $\alpha=0.05$ for 26 multiple comparisons.

Results

We collected 1416 Steller sea lion scat samples during 42 collection trips from 1986 through 2007. The number

of scat collected per trip ranged from 2 to 78 (mean of 34) (Table 1). Of the 1416 scat, 22 were discarded from analysis because they had no prey and 11 were discarded because they contained only unidentified prey, resulting in a working data set of 1383 scat. The majority of samples came from Rogue Reef during the breeding (n=526) and nonbreeding (n=290) seasons, followed by collections at the Columbia River South Jetty (n=219) and St. George Reef (n=165) during the breeding season. Only minor collections were made at Orford Reef during the breeding season (n=56), and Cascade Head (n=24) and St. George Reef (n=7) during the nonbreeding season (Table 1).

A total of 47 Steller sea lion prey taxa from 30 families were identified (33 to species) (Table 2). Overall percent frequency of occurrence for the most common (FO>10%) prey in decreasing order were Pacific hake (*Merluccius productus*, FO=78.6%), salmonids (*Oncorhynchus* spp.; FO=28.6%), skates (Rajidae; FO=23.4%), Pacific lamprey (*Lampetra tridentata*; FO=20.8%), clupeids (Clupeidae; FO=18.7%), rockfish (*Sebastes* spp.; FO=17.4%), northern anchovy (*Engraulis mordax*; FO=13.2%), and unidentified teleost fishes (FO=10.8%) (Table 2, Fig. 2). Scat during the breeding season were dominated by hake (87.1%), followed by salmonids (27.1%) and Pacific lamprey at 20.1%. Hake, with an FO of 59%, was also a primary prey in samples collected during the nonbreeding season and skate species increased in frequency to 40.3%, followed by salmonids (32.1%), and rockfish (29.7%) (Table 2). Prey diversity within scat samples ranged from one to 25 types, although 64% of all samples had ≤3 prey types. Of the 222 scat collected during the breeding season that contained a single prey item, 85.1% contained Pacific hake and 4.1% contained rockfish. Scat collected during the nonbreeding season that contained a single prey species (n=63), 49.2% contained hake and 22.2% rockfish.

By site and season (Fig. 2), Pacific hake occurred in more scats than any other prey taxa among all sites and seasons except at Cascade Head and St. George Reef during the nonbreeding season. For example, Pacific hake was the dominant prey in scats collected at Rogue Reef, the largest rookery in the study area, both during breeding (87.3%) and nonbreeding (62.1%) seasons. Although salmonids occurred with high frequency at all sites and seasons, except at Cascade Head, the highest frequency was found at Rogue Reef during the nonbreeding season. Skates, although consumed at all sites and seasons, occurred most frequently in scats collected during the nonbreeding season. For example, skate FO increased at Rogue Reef from 16.2% to 45.5% during the breeding and nonbreeding seasons, respectively. Pacific staghorn sculpin (*Leptocottus armatus*) was common only at the northern sites (i.e., Columbia River and Cascade Head), whereas rockfish were common only at the southern sites (particularly Rogue Reef).

In general, diet composition varied seasonally, annually, and spatially. After controlling for site and year (10 of 11 comparisons; Table 3), we found that diet differed by month; after controlling for site and month, we found that diet differed by year (10 of 12 comparisons; Table 4); and after controlling for year and month (2 of 3 comparisons; Table 5), we found that diet differed by site. Average Jaccard distance within collections ranged from 0.206 to 0.807 (median of 0.724), whereas average Jaccard distance between collections ranged from 0.425 to 0.911 (median of 0.771).

Discussion

Like other researchers (e.g., Pitcher, 1981; Merrick et al., 1997; Sinclair and Zeppelin, 2002; Womble and Sigler, 2006; Trites et al., 2007b; McKenzie and Wynne, 2008), we found that Steller sea lion diet was diverse yet dominated by only one or two species (Fig. 3). In Oregon and northern California the diet was dominated by Pacific hake, whereas in Alaska diet was dominated by walleye pollock (*Theragra chalcogramma*) in the Bering Sea and Gulf of Alaska, and Atka mackerel (*Pleurogrammus monopterygius*) in the Aleutians Islands. Prey types shared between Alaskan and Oregon–northern California collections included salmonids, clupeids (e.g., Pacific herring [*Clupea pallasii*]), rockfish, and skate.

The dominance of Pacific hake in Steller sea lion diets in Oregon and northern California is probably related to the widespread abundance of this species in the California current (as is the case with the widespread distribution of walleye pollock in Alaskan waters). Dorn et al.[2] reported that Pacific hake, ranging from southern California to the Queen Charlotte Sound, British Columbia, was the most abundant groundfish in the California Current system. During summer months adult Pacific hake move north along the Oregon coast while juveniles stay further south off central California (Bailey et al., 1982). From 1966 to 2007 the Pacific Coast (U.S, and Canadian waters) Pacific hake fishery landings averaged 219,000 metric tons (t), with a low of 90,000 t in 1980 and a peak harvest of 364,000 t in 2006 (Helser et al., 2008). Pacific hake are similar in caloric density to cod and pollock, which are prominent in the diet of Steller sea lions in the WDPS. This gadid diet has been hypothesized to result in chronic nutritional stress and ultimately population declines (Trites and Donnelly, 2003, Trites et al., 2007a). However, despite the dominance of Pacific hake in the diet from Oregon and northern California, Steller sea lions in the EDPS have been increasing at approximately 3% per year since the 1970s (Pitcher et al., 2007). This fact was cited by Fritz and Hinckley (2005) as evidence that was inconsistent with the nutritional stress hypothesis.

[2] Dorn, M. W., M. W. Saunders, C. D. Wilson, M. A. Guttormsen, K. Cooke, R. Kieser, and M. E. Wilkins. 1999. Status of the coastal Pacific hake/whiting stock in U.S. and Canada in 1998, 102 p. [Available at Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR. 97220 1384.]

Table 2

Sample information and frequency of occurrence (FO) of prey identified from Steller sea lion (*Eumetopias jubatus*) scat collected in Oregon and northern California from 1986 through 2007. FO is presented by collection site (CR=Columbia River, OR=Orford Reef, RR=Rogue Reef, and SGR=St. George Reef; CH=Cascade Head, see Fig. 1 and Table 1) and season (breeding=May–August, nonbreeding=September–April). Prey are sorted by family in decreasing order of total FO.

		Season		Breeding season				Nonbreeding season			
	Total	Breeding	Nonbreeding	CR	OR	RR	SGR	CR	CH	RR	SGR
Samples											
Total scat collected	1416	989	427	222	56	539	172	99	24	297	7
Scat containing ≥1 identifiable prey	1383	966	417	219	56	526	165	96	24	290	7
Scat containing no identifiable prey	11	6	5	0	0	4	2	0	0	5	0
Empty scat	22	17	5	3	0	9	5	3	0	2	0
Prey item											
Hakes: family Merlucciidae											
Pacific hake (*Merluccius productus*)	78.6	87.1	59.0	80.8	98.2	87.3	90.9	64.6	4.2	62.1	42.9
Salmon: family Salmonidae											
Pacific salmon (*Oncorhynchus* spp.)	28.6	27.1	32.1	27.9	21.4	27.6	26.7	22.9	4.2	37.9	14.3
Skate: family Rajidae											
Skate, unidentified	23.4	16.1	40.3	21.5	8.9	16.2	11.5	26.0	25.0	45.5	71.4
Lamprey: family Petromyzontidae											
Pacific lamprey (*Lampetra tridentata*)	20.8	20.1	22.3	12.3	3.6	28.5	9.1	19.8	0.0	25.2	14.3
Herring, shad, sardine: family Clupeidae											
Unidentified clupeid	18.7	17.7	20.9	27.4	7.1	14.8	17.6	18.8	37.5	20.3	14.3
Pacific herring (*Clupea pallasii*)	9.9	12.4	4.1	6.8	5.4	18.1	4.2	2.1	4.2	4.8	0.0
Pacific sardine (*Sardinops sagax*)	9.2	10.5	6.2	10.5	19.6	6.7	19.4	16.7	8.3	2.8	0.0
American shad (*Alosa sapidissima*)	2.2	1.9	3.1	4.6	1.8	1.1	0.6	5.2	8.3	2.1	0.0
Rockfish: family Sebastidae											
Rockfish (*Sebastes* spp.)	17.4	12.1	29.7	3.2	5.4	14.8	17.6	6.3	0.0	40.3	14.3
Anchovies: family Engraulidae											
Northern anchovy (*Engraulis mordax*)	13.2	11.9	16.1	33.8	8.9	4.2	8.5	24.0	33.3	11.4	42.9
Class Osteichthyes											
Teleost fishes, unidentified	10.8	10.1	12.5	5.9	5.4	11.6	12.7	13.5	4.2	12.8	14.3
Sculpins: family Cottidae											
Pacific staghorn sculpin (*Leptocottus armatus*)	9.4	7.2	14.4	26.5	1.8	1.7	1.2	35.4	54.2	4.5	0.0
Sculpins, unidentified	5.5	5.8	4.8	8.7	5.4	5.7	2.4	1.0	4.2	6.2	0.0
Irish lord (*Hemilepidotus* spp.)	1.6	2.0	0.7	0.0	1.8	1.1	7.3	0.0	0.0	1.0	0.0
Buffalo sculpin (*Enophrys bison*)	0.2	0.1	0.5	0.0	0.0	0.0	0.6	0.0	0.0	0.7	0.0
Sand lances: family Ammodytidae											
Pacific sand lance (*Ammodytes hexapterus*)	9.0	5.6	16.8	1.4	17.9	6.5	4.2	4.2	8.3	20.7	57.1

continued

Table 2 (continued)

		Season		Breeding season				Nonbreeding season			
	Total	Breeding	Nonbreeding	CR	OR	RR	SGR	CR	CH	RR	SGR
Smelts: family Osmeridae											
Smelts, unidentified	6.8	6.3	7.9	3.7	0.0	8.2	6.1	6.3	8.3	8.3	14.3
Eulachon (*Thaleichthys pacificus*)	0.1	0.0	0.2	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
Surf smelt (*Hypomesus pretiosus*)	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Stickleback: family Gasterosteidae											
Threespine stickleback (*Gasterosteus aculeatus*)	6.1	5.5	7.4	0.0	7.1	4.6	15.2	0.0	0.0	9.7	42.9
Squids and octopus: class Cephalopoda											
Squid and octopus, unidentified	5.7	5.6	6.0	0.5	3.6	6.8	9.1	3.1	0.0	7.6	0.0
Squids, unidentified	4.3	3.9	5.0	0.0	5.4	5.9	2.4	0.0	0.0	7.2	0.0
Octopus, unidentified	2.8	2.6	3.4	0.0	0.0	4.0	2.4	1.0	8.3	3.8	0.0
Jack mackerels: family Carangidae											
Pacific jack mackerel (*Trachurus symmetricus*)	5.4	7.1	1.2	2.3	14.3	5.9	15.2	1.0	0.0	1.4	0.0
Codfishes: family Gadidae											
Pacific tomcod (*Microgadus proximus*)	4.3	3.0	7.4	0.5	1.8	4.2	3.0	6.3	12.5	7.6	0.0
Codfishes, unidentified	1.5	1.2	2.2	0.0	0.0	1.3	3.0	1.0	0.0	2.8	0.0
Pacific cod (*Gadus macrocephalus*)	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Righteye flounders: family Pleuronectidae											
Starry flounder (*Platichthys stellatus*)	4.3	3.3	6.7	12.8	0.0	0.6	0.6	18.8	4.2	3.1	0.0
Dover sole (*Microstomus pacificus*)	2.1	2.1	2.2	3.2	0.0	1.7	2.4	0.0	0.0	3.1	0.0
Righteye flounder, unidentified	1.9	1.6	2.6	3.7	0.0	1.0	1.2	1.0	8.3	2.8	0.0
Rex sole (*Glyptocephalus zachirus*)	1.2	1.1	1.4	0.9	0.0	1.1	1.8	0.0	0.0	2.1	0.0
Sand sole (*Psettichthys melanostictus*)	1.2	0.8	2.2	0.5	0.0	1.0	1.2	2.1	0.0	2.4	0.0
Slender sole (*Lyopsetta exilis*)	1.2	1.0	1.7	0.0	0.0	0.8	3.6	0.0	0.0	2.4	0.0
Butter sole (*Isopsetta isolepis*)	1.2	0.6	2.4	0.5	0.0	0.8	0.6	4.2	4.2	1.4	14.3
English sole (*Parophrys vetulus*)	0.7	0.8	0.5	0.9	0.0	1.0	0.6	1.0	0.0	0.3	0.0
Arrowtooth flounder (*Atheresthes stomias*)	0.1	0.1	0.2	0.0	0.0	0.0	0.6	1.0	0.0	0.0	0.0
Rock sole (*Lepidopsetta bilineata*)	0.1	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Flatfishes: order Pleuronectiformes											
Flatfishes, unidentified	3.1	2.6	4.3	2.3	1.8	3.2	1.2	5.2	4.2	3.8	14.3
Dogfish sharks: family Squalidae											
Spiny dogfish (*Squalus acanthias*)	2.7	2.8	2.4	5.0	0.0	2.5	1.8	2.1	0.0	2.8	0.0
Sanddabs: family Paralichthyidae											
Sanddabs (*Citharichthys* spp.)	2.7	2.2	4.1	2.3	0.0	1.7	4.2	5.2	20.8	2.1	14.3
Hagfishes: family Myxinidae											
Pacific hagfish (*Eptatretus stoutii*)	1.6	2.1	0.5	0.0	0.0	2.9	3.0	0.0	0.0	0.7	0.0

continued

Table 2 (continued)

		Season		Breeding season				Nonbreeding season			
	Total	Breeding	Nonbreeding	CR	OR	RR	SGR	CR	CH	RR	SGR
Mackerel and tuna: family Scombridae											
Pacific chub mackerel (*Scomber japonicus*)	1.4	2.1	0.0	0.0	0.0	3.4	1.2	0.0	0.0	0.0	0.0
Greenlings: family Hexagrammidae											
Greenling/lingcod, unidentified	0.7	0.8	0.2	0.0	1.8	0.6	2.4	0.0	0.0	0.0	14.3
Lingcod (*Ophiodon elongatus*)	1.3	0.6	2.9	0.0	0.0	1.0	0.6	1.0	4.2	3.4	0.0
Greenling (*Hexagrammos* spp.)	0.3	0.2	0.5	0.0	0.0	0.0	1.2	1.0	0.0	0.3	0.0
Poachers: family Agonidae											
Poachers, unidentified	1.3	1.6	0.7	3.7	0.0	0.4	3.0	1.0	0.0	0.7	0.0
Sturgeon poacher (*Podothecus accipenserinus*)	0.1	0.1	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Subclass Elasmobranchii											
Sharks and rays, unidentified	1.2	1.3	1.0	3.7	0.0	0.8	0.6	1.0	0.0	1.0	0.0
Sharks, unidentified	0.3	0.1	0.7	0.0	0.0	0.2	0.0	0.0	0.0	1.0	0.0
Surfperch: family Embiotocidae											
Surfperch, unidentified	1.1	0.7	1.9	0.0	0.0	1.1	0.6	3.1	0.0	1.7	0.0
Gunnel: family Pholidae											
Gunnel, unidentified	1.0	0.9	1.2	0.5	0.0	0.8	2.4	0.0	0.0	1.7	0.0
Wolffishes: family Anarhichadidae											
Wolf eel (*Anarrhichthys ocellatus*)	0.8	1.1	0.0	0.0	1.8	1.3	1.8	0.0	0.0	0.0	0.0
Snailfish: family Liparidae											
Snailfish and lumpfish, unidentified	0.7	0.9	0.2	1.4	1.8	1.0	0.0	0.0	0.0	0.3	0.0
Cusk-eels: family Ophidiidae											
Spotted cusk-eel (*Chilara taylori*)	0.3	0.3	0.2	0.0	0.0	0.2	1.2	0.0	0.0	0.3	0.0
Prickleback: family Stichaeidae											
Pricklebacks, unidentified	0.3	0.4	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0
Class Agnatha											
Jawless fishes, unidentified	0.1	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Clingfish: family Gobiesocidae											
Clingfishes, unidentified	0.1	0.2	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
Northern clingfish 0.1 (*Gobiesox maeandricus*)	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	
Eelpout: family Zoarcidae											
Eelpouts, unidentified	0.1	0.1	0.2	0.0	0.0	0.0	0.6	0.0	0.0	0.3	0.0
Pipefish: family Syngnathidae											
Bay pipefish (*Syngnathus leptorhynchus*)	0.1	0.1	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Sandfish: family Trichodontidae											
Pacific sandfish (*Trichodon trichodon*)	0.1	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Sandfishes, unidentified	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0

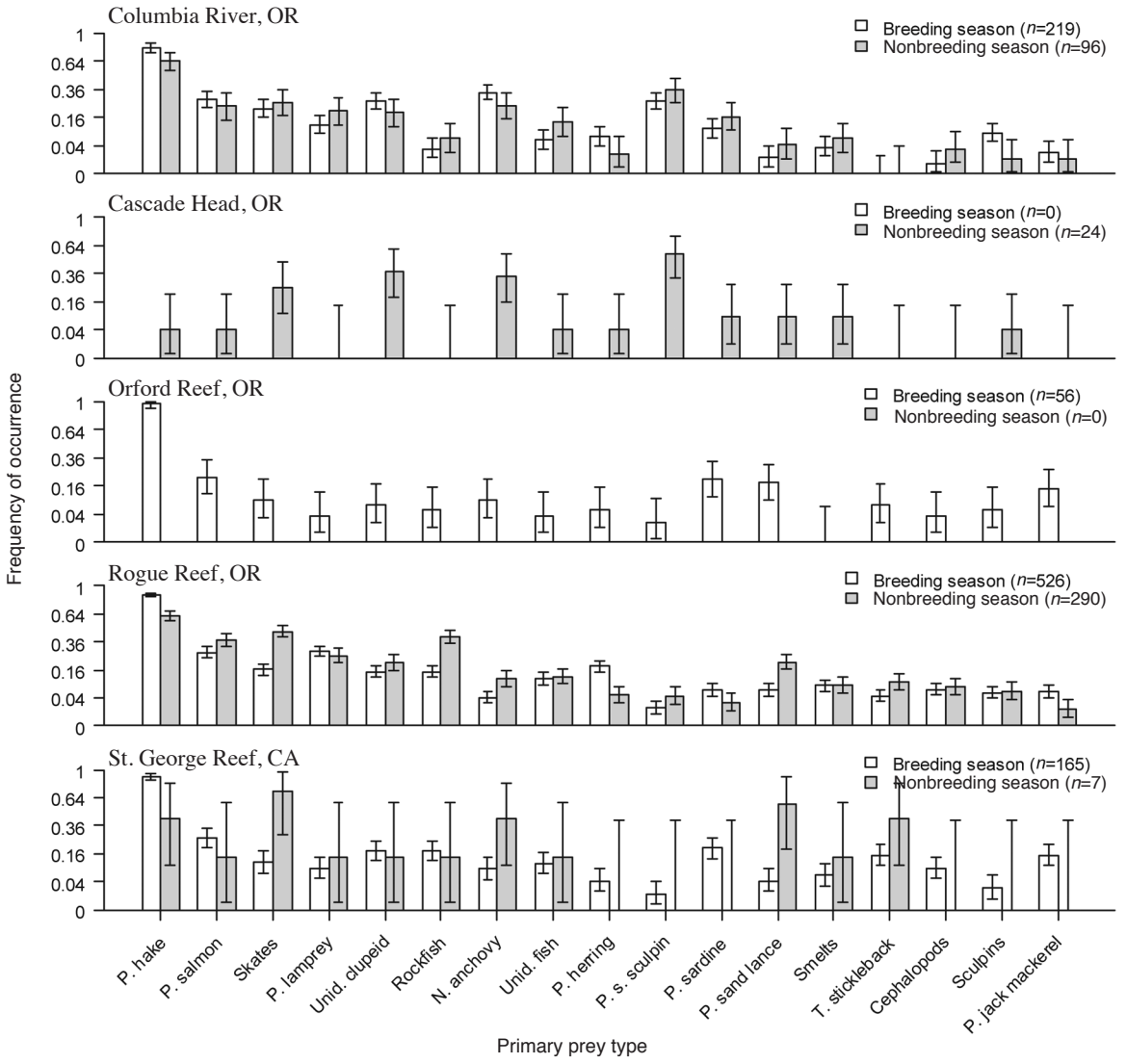

Figure 2

Frequency of occurrence (FO) of primary prey (prey with total FO values≥0.05) identified from Steller sea lion (*Eumetopias jubatus*) scat collected in Oregon and northern California from 1986 through 2007. FO is presented by collection site and season (breeding season=May–August, nonbreeding season=September–April) in descending order of overall pooled FO. Error bars indicate exact 95% binomial confidence intervals. Scientific names for prey types can be found in Table 1. P=Pacific; N=northern; s=staghorn; T=threespine.

How important a specific type of prey is to the survival of an opportunistic marine pinniped predator is unknown. Abundance of prey may have more impact on survival when a predator feeds on schooling fish rather than on more solitary types of prey, such as flatfish and sculpin. Furthermore, a diversity of prey types may be important in sustaining populations and help buffer the effects of ocean climate changes. For example, analyses by Merrick et al. (1997) and Trites et al. (2007b) showed a strong positive correlation between diet diversity and rate of population change. Our data are consistent with this finding; we identified 17 primary (≥5%) prey types (Fig. 3) and the population has been growing at approximately 3% per year (Pitcher et al., 2007).

Perhaps as a reflection of their diverse diet, we found a surprisingly high number of statistical differences in diet composition between months (Table 3), years (Table 4), and sites (Table 5). Although simulation exercises (not presented) indicated that the Mantel test was not overly sensitive (e.g., it did not reject a null hypothesis simply due to a large difference in a single prey type), the procedure is only a hypothesis test and does not lend itself to estimation of effect sizes or biologically

Table 3

Comparison of Steller sea lion (*Eumetopias jubatus*) diet composition by month, after controlling for collection site and year. Sample size (n=number of scat analyzed) and individual number of prey types (D) are given for each diet; pooled number of unique prey types (D_p), correlation coefficient (R_M), and permutation-based P-value (based on 9999 replications) are given for each comparison. * indicates significance at the a=0.002 level (based on Bonferroni adjustment of α=0.05 for 26 multiple comparisons).

		Diet 1			Diet 2				Mantel test	
Site	Year	Month	n	D	Month	n	D	D_p	R_M	P value
Columbia R.	2004	June	53	25	August	37	13	27	0.061	0.0017*
		June	53	25	September	43	17	28	0.145	0.0001*
		August	37	13	September	43	17	19	0.047	0.0105
Rogue Reef	2001	April	45	32	August	48	32	44	0.089	0.0001*
	2002	March	39	27	April	49	30	36	0.264	0.0001*
		March	39	27	July	33	27	35	0.409	0.0001*
		March	39	27	August	37	35	38	0.251	0.0001*
		April	49	30	July	33	27	36	0.173	0.0001*
		April	49	30	August	37	35	39	0.147	0.0001*
		July	33	27	August	37	35	40	0.117	0.0002*
	2003	April	57	29	October	53	31	42	0.101	0.0001*

Table 4

Comparison of Steller sea lion (*Eumetopias jubatus*) diet composition by year, after controlling for collection site and month. Sample size (n) and individual number of prey types (D) are given for each diet; pooled number of unique prey types(D_p), correlation coefficient (R_M), and permutation-based P-value (based on 9999 replications) are given for each comparison. * indicates significance at the α=0.002 level (based on Bonferroni adjustment of α=0.05 for 26 multiple comparisons).

		Diet 1			Diet 2				Mantel test	
Site	Month	Year	n	D	Year	n	D	D_p	R_M	P value
Columbia R.	August	2004	37	13	2007	31	16	20	0.105	0.0004*
Rogue Reef	April	2001	45	32	2002	49	30	40	0.109	0.0001*
		2001	45	32	2003	57	29	40	0.018	0.0682
		2002	49	30	2003	57	29	38	0.126	0.0001*
	June	1987	34	14	1993	36	29	32	0.222	0.0001*
	July	1990	43	16	2002	33	27	29	0.199	0.0001*
		1990	43	16	2004	33	20	26	0.216	0.0001*
		2002	33	27	2004	33	20	29	0.097	0.0001*
	August	2001	48	32	2002	37	35	41	0.123	0.0001*
St. George Reef	July	2002	33	13	2004	33	21	22	0.008	0.2515
		2002	33	13	2006	33	21	25	0.122	0.0001*
		2004	33	21	2006	33	21	29	0.203	0.0001*

interpretable parameters. Nonetheless, it does indicate that researchers should be cautious about pooling samples across space and time before investigating whether those samples differ.

Athough analysis of pinniped fecal matter is a standard technique for studying diet (e.g., Pitcher, 1980; Beach et al.[3]; Olesiuk et al., 1990; Orr et al., 2004), there are some limitations. For example, the use of otoliths to identify prey can lead to biased diet composition estimates (Jobling and Breiby, 1986). We minimized this problem by including all bony skeletal structures (vertebrae, gillrakers, etc.) to identify prey. Another potential bias can occur when drawing inference to a particular population from opportunistically collected

[3] Beach, R. J., A.C. Greiger, S. J. Jeffries, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982: third annual report, March 1, 1980 to October 31, 1982. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, NMFS, NOAA Proc. Rep. 85-03, 316 p. [Available at www.lib.noaa.gov, accessed May 2011.]

Table 5

Comparison of Steller sea lion (*Eumetopias jubatus*) diet composition by site, after controlling for collection year and month. Sample size (n) and individual number of prey types (D) are given for each diet; pooled number of unique prey types(D_p), correlation coefficient (r_M), and permutation-based P-value (based on 9999 replications) are given for each comparison. * Indicates significance at the α=0.002 level (based on Bonferroni adjustment of α=0.05 for 26 multiple comparisons).

		Diet 1			Diet 2				Mantel test	
Year	Month	Site	n	D	Site	n	D	D_p	r_M	P value
1990	July	Orford Reef	41	6	Rogue Reef	43	16	17	0.079	0.0002*
2002	July	Rogue Reef	33	27	St. George Reef	33	13	28	0.075	0.0023
2004	July	Rogue Reef	33	20	St. George Reef	33	21	25	0.096	0.0008*

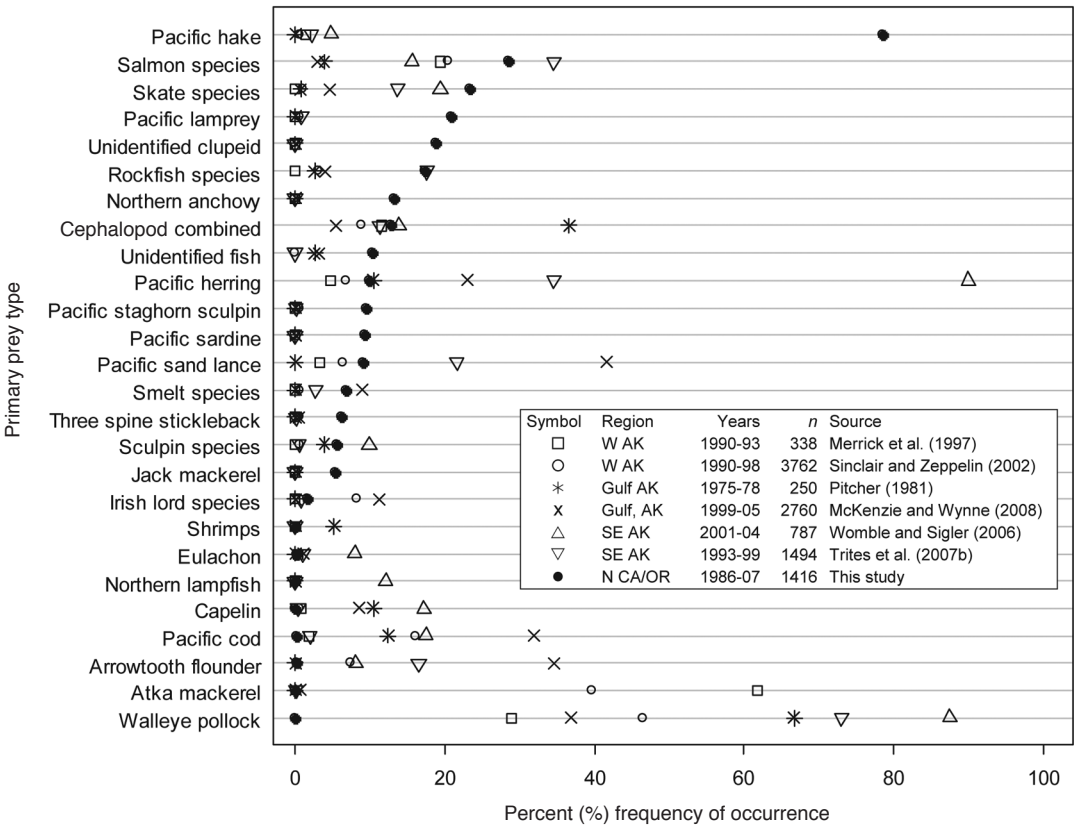

Figure 3

Percent frequency of occurrence (FO) of primary prey reported for Steller sea lions (*Eumetopias jubatus*) in Alaska (n=6 studies) and northern California and Oregon (this study). FO summary for Trites et al. (2007b) and Merrick et al. (1997) was calculated by the authors of the present study. Scientific names for prey types can be found in Table 1.

samples. For example, scat that we collected on rookeries (i.e., Rogue Reef, Orford Reef, St. George Reef) during the summer breeding season primarily reflect adult female diet because males often fast during the breeding season and juveniles are not generally present at rookery sites.

The Steller sea lion recovery plan (NMFS, 2008) notes that although several factors affecting the endangered WDPS also affect the threatened EDPS, those threats do not appear to be affecting the sustained growth or recovery of the EDPS. It is noted in the plan, however, that concerns regarding climate change,

particularly on the southern part of the species range, warranted continued research and monitoring. Population growth in California sea lions (Carretta et al., 2010) may also be a concern for the EDPS because these sympatric ottariids potentially compete for prey resources and habitat. Steller sea lions in the Channel Island rookeries in California experienced a similar situation in the late 1950s as California sea lion populations increased and potentially out-competed Steller sea lions for food and habitat (Bartholomew and Boolootian, 1960). Additionally, as the Steller sea lion EDPS increases, its real and perceived impacts on sport and commercial fish harvests; as well as threatened and endangered fish populations, will likely increase. For example, Steller sea lion abundance at Bonneville Dam on the Columbia River (Fig. 1), 235 km from the ocean, increased from zero individuals in 2002 to at least 53 in 2010 and these sea lions have consumed hundreds of threatened and endangered salmonids and thousands of white sturgeon (*Acipenser transmontanus*) (Stansell et al.[4]). Ongoing uncertainties over the role of diet in the decline of the WDPS, impacts of climate change on the EDPS, and emerging management concerns all argue for continued and refined research on Steller sea lion diet and foraging behavior in the southern extent of their range.

Conclusions

Identification of prey from 1383 Steller sea lions scats collected in Oregon and northern California during 1986–2007 resulted in a list of 47 prey taxa consumed. Primary prey items included Pacific hake, Pacific salmon, skate, Pacific lamprey, rockfish and clupeid species. Prey identified from scat during the breeding and nonbreeding seasons were fairly similar but rockfish and skate species had a higher frequency of occurrence during the nonbreeding season. Data analysis showed that, in general, diet composition varied seasonally, annually, and spatially. When compared to previous diet studies for Steller sea lions in Alaska, this population was shown to depend on hake as the primary prey rather than on the gadid and hexagrammid species identified in the northern populations studied. Salmonids were important prey in all the studies compared. Continued study of Steller sea lion food habits is necessary to evaluate their interactions with important fish populations (such as salmonids and rockfish), to assess the increasing pressure from migrating California sea lions for limited prey resources, and to begin to address the effects of climate change on population abundance.

[4] Stansell, R. J, K. M. Gibbons, and W. T. Nagy. 2010. Evaluation of pinniped predation on adult salmonids and other fish in the Bonneville Dam tailrace, 2008–2010. U.S. Army Corps of Engineers, Cascade Locks, OR. [Available online at http://www.nwd-wc.usace.army.mil/tmt/documents/fish/2010/2008-2010_Pinniped_Report.pdf, accessed 2 March 2011.]

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