

Spatial and temporal variation in the diet of Steller sea lions in the Kodiak Archipelago, 1999 to 2005

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ABSTRACT: Spatial and temporal variation in the diet of Steller sea lions *Eumetopias jubatus* was investigated using scat (fecal) samples collected from 4 regions in the Kodiak Archipelago. Over 2700 scats with identifiable prey were collected from the northern, eastern, southern and western sides of Kodiak Island from 1999 to 2005. Of 76 prey types identified using hard remains, the most important species in terms of frequency of occurrence and numerical abundance were Pacific sand lance *Ammodytes hexapterus*, walleye pollock *Theragra chalcogramma*, arrowtooth flounder *Atheresthes stomias*, Pacific cod *Gadus macrocephalus*, salmon *Oncorhynchus* spp., and Pacific herring *Clupea pallasii*. Significant differences in diet composition were found among regions, seasons, and years, suggesting that the diet of sea lions is strongly influenced by local and temporal distributions and abundances of prey. Herring dominated scat collections from the west coast and accounted for most (14 to 30%) of the differences in regional diet in spring and winter. Annual variation in diet was relatively low in winter, whereas spring and fall diets varied from year to year, with regional-specific shifts in dominant prey. Results from our study generally agree with diet studies conducted in the 1990s, but differ markedly in the relative importance of the major prey species.

KEY WORDS: *Eumetopias jubatus* · Prey · Seasonal · Diet overlap · Forage fish · Gulf of Alaska · *Theragra chalcogramma* · *Ammodytes hexapterus*

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INTRODUCTION

Steller sea lions *Eumetopias jubatus* are distributed along the North Pacific Rim from northern Japan to central California. The population is divided into 2 genetically distinct population segments (DPSs), the western and eastern DPS, with the boundary near Cape Suckling (144°W) in the Gulf of Alaska (Loughlin 1997). Between the early 1970s and 2000, the western DPS within Alaska declined by approximately 85% (Sease et al. 2001), prompting the western population to be listed as 'endangered' under the US Endangered Species Act in 1997. From 1991 to 2000 the average annual rate of decline was approximately 5.4% (Loughlin & York 2000), but between 2000 and 2004 the decline appears to have abated in some areas (Fritz & Stinchcomb 2005). In contrast, the eastern DPS increased at an average annual rate of 3.2% between 1979 and 2005 (Pitcher et al. 2007) and is currently

listed as 'threatened'. The cause or causes of the decline of the western population are unclear. Most hypotheses focus on the effects of a shift in prey availability and composition on the foraging ecology, reproduction and survival of sea lions (DeMaster & Atkinson 2002, Trites et al. 2007a). Other factors, such as predation by killer whales and incidental take in commercial fisheries may also play a role (National Research Council 2003).

To investigate the impact of changing prey availability on sea lion populations, a number of bioenergetics and trophic models have been developed that explore the relationships between the food requirements of Steller sea lions and the possible impact of commercial fisheries, competition with other species, and ecosystem change (e.g. Winship & Trites 2003, Guénette et al. 2006). Critical to the development of such models are data on the diet of Steller sea lions. Diet composition of Steller sea lions is known to vary geographically and

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seasonally (Sinclair & Zeppelin 2002, Waite & Burkanov 2006). However, due to insufficient data most models have assumed that diet remains constant throughout the year and is similar over broad geographic areas. Recent diet studies in southeast Alaska have indicated considerable spatial, seasonal, and interannual variability in diet over a relatively fine scale (Womble & Sigler 2006, Trites et al. 2007b). However, fine-scale dietary studies are lacking in western Alaska. These models are also largely based on diet information collected in the 1990s, and therefore may not fully reflect the current status of Steller sea lions in the Gulf of Alaska.

Steller sea lion diet assessment has focused on identifying prey remains in stomach and fecal samples. Prior to the 1990s, Steller sea lion diets were assessed by examination of stomach contents of shot animals, and just over 400 stomachs were collected from 1945 to 1986 (Imler & Sarber 1947, Mathisen et al. 1962, Thorsteinson & Lensink 1962, Fiscus & Baines 1966, Pitcher 1981, Lowry et al. 1982). Considerable effort was made in the 1990s to assess the diet of Steller sea lions in the western range, with the collection of over 3700 scat (fecal) samples throughout the Aleutian Islands and central Gulf of Alaska (Merrick et al. 1997, Sinclair & Zeppelin 2002). However, individual site-specific collections were small in number and pooled within 2 broad seasons and across years within data-defined geographical areas. These studies identified a wide range of prey and demonstrated regional and seasonal differences in diet composition across the western range of the population. Comparisons of individual site collections also suggested that, with larger sample sizes, important spatial and temporal differences in diet may be found at a finer scale.

A number of factors may influence the degree of variation in diet composition within and among studies such as sampling techniques (scats vs. stomach contents), sample distribution (sites, months, years), the sex and age of animals from which samples are derived, and interannual variability in prey availability. Despite sampling limitations of historical data, it has been suggested that the diet of Steller sea lions in western Alaska switched from mostly small energy-rich schooling fishes (such as herring, capelin, and sand lance) prior to the 1970s, to mostly gadid species (such as walleye pollock) in the Gulf of Alaska and Atka mackerel in the Aleutians in the 1980s and 1990s (Merrick et al. 1997, Sinclair & Zeppelin 2002). It was also proposed that diet diversity was lowest where the sharpest decline in the Steller sea lion populations occurred (Merrick et al. 1997), and that diet diversity was a proxy for overall energy content of diet, with low diet diversity equating to low energy content (Winship & Trites 2003). However, to distinguish between back-

ground variation and variation that constitutes an ecologically important change, a greater understanding of the temporal and spatial variation in sea lion diet is required. This requires focused studies that limit temporal and spatial variation in data by standardizing collection efforts and evaluating diet at a finer scale.

The Kodiak Archipelago is located in the west-central Gulf of Alaska, where population numbers appear to have continued to decline through 2004, although at a slower rate since 1999 (Fritz & Stinchcomb 2005). Steller sea lions utilize a number of terrestrial sites throughout the archipelago and, as central-place foragers, are likely to be influenced by spatial and temporal availability of prey at a local level. The shelf, coastal, and inside waters of the Kodiak Archipelago present a mosaic of marine habitats, from shallow nearshore areas at the heads of long fjords to deep areas subject to strong tidal currents. Productivity and biodiversity in the region are also influenced by 2 main southwest-flowing current systems: the Alaskan Coastal Current, which passes to the west of Kodiak through the Shelikof Strait, and the Alaskan Stream, which passes along the northeastern coast. Species composition of fish communities on the continental shelf and in nearshore waters around Kodiak Island and adjacent areas vary spatially, but can also change over relatively short periods of time (Anderson & Piatt 1999, Robards et al. 1999a, Mueter & Norcross 2000a). We therefore expected that the diet of Steller sea lions in the Kodiak area would vary spatially and temporally on a relatively fine scale.

The specific objectives of our study were (1) to describe the diet of Steller sea lions in the Kodiak Archipelago based on analysis of scats collected between 1999 and 2005 and (2) to assess the extent of geographical, seasonal, and interannual variability in diet. This information will be integrated into future studies to explore relationships between prey availability, diet composition, and haulout use. The data presented will also assist in the refinement of biomass and consumption models for Steller sea lions and will facilitate fine-scale evaluation of the overlap between sea lions and commercial fisheries in the Kodiak region.

MATERIALS AND METHODS

Sample collection and processing. The Kodiak Archipelago (57° 28' N, 153° 25' W) is approximately 240 km long, extending from Shuyak Island in the north to the Trinity Islands in the south, and is separated from the Alaskan Peninsula by the Shelikof Strait, which averages 48 km in width. Scats were collected from 8 haulouts (non-breeding areas) and 2 rookeries (breeding areas) in the Kodiak region (Fig. 1) between September 1999 and

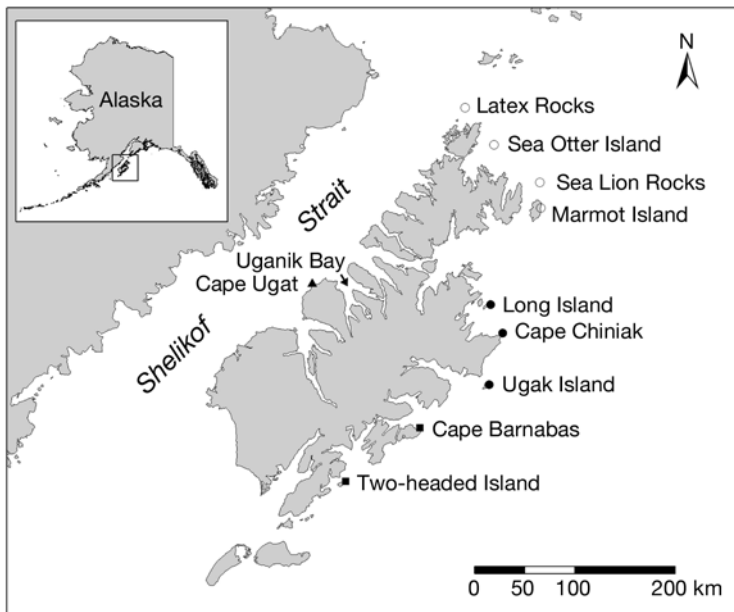


Fig. 1. Sites where Steller sea lion scats were collected in the Kodiak Archipelago from 1999 to 2005. Sites were grouped into 4 geographical regions; north (○), east (●), south (■), and west (▲)

March 2005. Most sites are used year-round by varying numbers of sea lions of mixed age and sex classes, except for Long Island and Cape Barnabas, which are generally vacated during the summer months (June to August) and Ugak Island, which is used only in summer (Wynne 2005). The 2 rookeries (Marmot and Two-Headed Island) are also used as haulouts by mixed age and sex classes during the non-breeding season. Samples were not collected from Marmot and Two-Headed Island during the peak of the breeding season (June), and were collected only once in July from Two-Headed. Therefore, we assessed the diet of non-breeding mixed age and sex classes. To investigate geographical variation in diet, scats collected from individual sites were pooled into 4 spatial groups based on proximity: north (Latex Rocks, Sea Otter Rocks, Sea Lion Rocks, and Marmot Island), east (Long Island, Cape Chiniak, and Ugak Island), south (Cape Barnabas and Two-Headed Island), and west (Cape Ugat) (Fig. 1). Although individual sea lions may move among sites (Merrick & Loughlin 1997), we have assumed that sea lions haul out at sites closest to or within their most recent foraging area. Thus, scats

deposited at sites were assumed to reflect prey consumed in the local area. Scat collections were made monthly, but not all sites or regions were visited each month or season due to logistics, weather conditions, and the need to minimize disturbance (Table 1). Monthly collections were pooled into 4 standard seasons: winter (December to February), spring (March to May), summer (June to August), and fall (September to November), with winter marking the start of a new annual collection. Seasonal collections were complete between 2000 and 2003, but were limited to fall in 1999, winter and fall in 2004, and spring in 2005. For analysis, samples pooled within spatial groups and within seasons were treated as a single collection.

Each scat was placed in a separate plastic bag and frozen at -20°C until processed. Prey remains were separated by soaking thawed scats in soapy water for at least 1 d, and then washing each sample through nested sieves (1.4, 0.7, and 0.5 mm). All hard remains were recovered and stored dry. Diagnostic structures were identified by

Pacific Identifications (Victoria, BC, Canada) to the lowest taxonomic level possible by comparison with reference collections. Taxonomic information for prey identified is provided in Table 2. For each scat, the

Table 1. Number of Steller sea lion scat samples with identifiable prey collected from 4 regions in the Kodiak archipelago (1999 to 2005). For analysis, annual collections commenced in December (winter) of the previous calendar year. Small collections (<23 scats) were not used in analysis of spatial and temporal variation in diet composition

Year	Season	North	East	South	West	Total
1999	Fall	27	24	23	26	100
2000	Winter	119	84	0	39	242
	Spring	52	57	0	2	111
	Summer	73	18	62	0	153
2001	Fall	38	65	13	0	116
	Winter	110	90	0	35	235
	Spring	55	19	0	48	122
2002	Summer	77	0	27	6	110
	Fall	203	76	0	39	318
	Winter	28	25	0	31	84
2003	Spring	51	53	0	34	138
	Summer	34	15	14	53	116
	Fall	177	44	31	48	300
2004	Winter	0	76	0	0	76
	Spring	48	54	0	43	145
	Summer	75	0	30	17	122
2005	Fall	12	26	0	0	38
	Winter	0	29	0	58	87
	Fall	46	0	0	0	46
2005	Spring	0	52	0	49	101
Total	1999–2005	1225	807	200	528	2760

prey type present, minimum number of individual prey, and relative size class of prey were recorded. Empty scats or scats containing only unidentifiable prey were excluded from analysis.

The minimum number of individual prey items (MNI) was estimated as the greatest number of either paired (e.g. otoliths, upper or lower cephalopod beaks, and hypobranchial) or unique structures. Samples that contained only non-unique remains (e.g. non-unique vertebra, teeth, and scales) were recorded as containing a single individual (Browne et al. 2002). Enumer-

ated prey were also assigned to relative fork length size (FL cm) ranges by Pacific Identifications by comparing diagnostic bone structures with those of a reference collection and a subjective assessment of the level of digestion. To assess the size of prey consumed, prey of a given size range were recorded as present or absent in scat samples, and only data from scats with bone structures in good (pristine to minimal erosion) or fair (moderate erosion not affecting diagnostic features) condition were used. Due to the subjective nature of the size classification and use of overlapping

Table 2. Overall percentage frequency of occurrence (FO), relative occurrence (RO), relative abundance (RA), and index of importance (IIMP) of prey identified in Steller sea lion scats collected from sites in the Kodiak Archipelago (1999 to 2005). Prey highlighted in bold occurred with $\geq 10\%$ FO in any single collection. Prey with values of 0.0 indicate actual value was < 0.1

Prey identified	FO	RO	RA	IIMP
Poachers: family Agonidae	0.5	0.2	0.1	0.1
Sand lances: family Ammodytidae				
Pacific sand lance (<i>Ammodytes hexapterus</i>)	41.7	13.2	38.6	16.1
Sablefishes: family Anoplopomatidae				
Sablefish (<i>Anoplopoma fimbria</i>)	0.8	0.2	0.1	0.2
Tubesnout: family Aulorhynchidae				
Tubesnout (<i>Aulorhynchus flavidus</i>)	0.7	0.2	0.1	0.1
Deep sea smelts: family Bathylagidae				
Northern smooth tongue (<i>Leuroglossus schmidti</i>)	0.0	0.0	0.0	0.0
Ronquils: family Bathymasteridae				
Searcher (<i>Bathymaster signatus</i>)	0.1	0.0	0.0	0.0
Unidentified ronquils (Bathymasteridae)	0.2	0.1	0.0	0.0
Northern ronquil (<i>Ronquilus jordani</i>)	0.1	0.0	0.0	0.0
Herring: family Clupeidae				
Pacific herring (<i>Clupea pallasii</i>)	23.0	7.3	6.3	7.7
Sculpins: family Cottidae				
<i>Artedius</i> spp.	0.0	0.0	0.0	0.0
Unidentified sculpins	3.8	1.2	0.5	0.8
Armorhead sculpin (<i>Gymnocanthus galeatus</i>)	0.0	0.0	0.0	0.0
Red Irish lord (<i>Hemilepidotus hemilepidotus</i>)	0.3	0.1	0.0	0.1
Yellow Irish lord (<i>Hemilepidotus jordani</i>)	0.1	0.0	0.0	0.0
Unidentified Irish lord (<i>Hemilepidotus</i> spp.)	10.8	3.4	1.6	2.4
Plain sculpin (<i>Myoxocephalus jaok</i>)	0.1	0.0	0.0	0.0
<i>Triglops</i> spp.	0.0	0.0	0.0	0.0
Lumpsuckers: family Cyclopteridae				
Smooth lumpsucker (<i>Aptocyclus ventricosus</i>)	0.5	0.1	0.1	0.1
Unidentified lumpsuckers	1.3	0.4	0.2	0.3
Sleeper sharks: family Dalatiidae				
Pacific sleeper shark (<i>Somniosus pacificus</i>)	0.0	0.0	0.0	0.0
Anchovy: family Engraulidae				
Anchovy (<i>Engraulis mordax</i>)	0.0	0.0	0.0	0.0
Cods: family Gadidae				
Saffron cod (<i>Eleginus gracilis</i>)	0.1	0.0	0.0	0.0
Unidentified gadids (Gadidae)	10.3	3.3	1.8	3.3
Pacific cod (<i>Gadus macrocephalus</i>)	31.9	10.1	5.6	9.5
Pacific tomcod (<i>Microgadus proximus</i>)	0.1	0.0	0.0	0.0
Walleye pollock (<i>Theragra chalcogramma</i>)	36.8	11.6	10.9	15.1
Sticklebacks: family Gasterosteidae				
Threespine stickleback (<i>Gasterosteus aculeatus</i>)	0.4	0.1	0.1	0.1
Sailfin sculpins: family Hemitriptidae	0.0	0.0	0.0	0.0
Greenlings: family Hexagrammidae				
Unidentified greenlings	0.5	0.2	0.1	0.1
Hexagrammos spp.	2.5	0.8	0.5	0.5
Kelp greenling (<i>Hexagrammos decagrammus</i>)	0.1	0.0	0.0	0.0
Rock greenling (<i>Hexagrammos lagocephalus</i>)	1.4	0.4	0.2	0.2
Atka mackerel (<i>Pleurogrammus monopterygius</i>)	0.7	0.2	0.1	0.2

Table 2 (continued)

Prey identified	FO	RO	RA	IIMP
Snailfishes: family Liparidae	6.2	2.0	1.1	1.8
Lanternfishes: family Myctophidae				
Northern lampfish (<i>Stenobrachius leucopsarus</i>)	0.0	0.0	0.0	0.0
Smelts: family Osmeridae				
Surf smelt (<i>Hypomesus pretiosus</i>)	0.1	0.0	0.0	0.0
Capelin (<i>Mallotus villosus</i>)	8.6	2.7	7.9	3.9
Unidentified smelt	8.9	2.8	1.3	2.1
Eulachon (<i>Thaleichthys pacificus</i>)	1.1	0.3	0.2	0.2
Gunnels: family Pholidae				
Penpoint gunnel (<i>Apodichthys flavidus</i>)	0.0	0.0	0.0	0.0
Unidentified gunnel	1.9	0.6	0.3	0.3
Crescent gunnel (<i>Pholis laeta</i>)	0.4	0.1	0.1	0.1
Flatfish: order Pleuronectiformes				
Arrowtooth flounder (<i>Atheresthes stomias</i>)	34.7	11.0	5.6	12.5
Rex sole (<i>Glyptocephalus zachirus</i>)	0.1	0.0	0.0	0.0
Flathead sole (<i>Hippoglossoides elassodon</i>)	0.1	0.0	0.0	0.0
Pacific halibut (<i>Hippoglossus stenolepis</i>)	2.9	0.9	0.4	0.9
Rock sole (<i>Lepidopsetta</i> spp.)	6.7	2.1	1.0	1.5
Yellowfin sole (<i>Limanda aspera</i>)	0.0	0.0	0.0	0.0
Sand sole (<i>Lyopsetta exilis</i>)	0.0	0.0	0.0	0.0
Dover sole (<i>Microstomus pacificus</i>)	0.2	0.1	0.0	0.0
Starry flounder (<i>Platichthys stellatus</i>)	0.9	0.3	0.1	0.1
Alaska plaice (<i>Pleuronectes quadrituberculatus</i>)	0.0	0.0	0.0	0.0
Unidentified flatfish	8.7	2.8	1.2	2.2
Sand sole (<i>Psettichthys melanostictus</i>)	0.2	0.1	0.0	0.0
Skates: family Rajidae	4.6	1.5	0.6	1.0
Salmonids: family Salmonidae				
Pacific salmon (<i>Oncorhynchus</i> spp.)	26.3	8.3	4.3	8.4
Dolly varden (<i>Salvelinus malma</i>)	0.1	0.0	0.0	0.0
Rockfishes: family Scorpaenidae				
Unidentified rockfish (Scorpaenidae)	0.7	0.2	0.1	0.2
Rockfish (<i>Sebastes</i> spp.)	3.6	1.1	0.5	0.7
Thornyheads (<i>Sebastolobus</i> spp.)	0.0	0.0	0.0	0.0
Dogfish sharks: family Squalidae				
Spiny dogfish (<i>Squalus acanthias</i>)	0.9	0.3	0.1	0.2
Pricklebacks: family Stichaeidae				
High cockscomb (<i>Anoplarchus purpurescens</i>)	0.5	0.1	0.1	0.1
Snake prickelback (<i>Lumpenus sagitta</i>)	0.0	0.0	0.0	0.0
Unidentified pricklebacks (Stichaeidae)	1.3	0.4	0.2	0.2
Arctic shanny (<i>Stichaeus punctatus</i>)	0.0	0.0	0.0	0.0
Black prickelback (<i>Xiphister atropurpureus</i>)	0.0	0.0	0.0	0.0
Rock prickelback (<i>Xiphister mucosus</i>)	0.0	0.0	0.0	0.0
Prickelback (<i>Xiphister</i> spp.)	0.1	0.0	0.0	0.0
Sandfishes: family Trichodontidae				
Pacific sandfish (<i>Trichodon trichodon</i>)	10.5	3.3	2.8	2.5
Eelpouts: family Zoarchidae				
Shortfin eelpout (<i>Lycodes brevipes</i>)	0.0	0.0	0.0	0.0
Wattled eelpout (<i>Lycodes palearis</i>)	0.0	0.0	0.0	0.0
Unidentified fish spp.	3.1	1.0	0.4	1.0
Squids and octopus: Order Cephalopoda				
Unidentified cephalopods	2.1	0.7	0.3	0.4
Octopus spp.	2.8	0.9	0.4	0.6
Squid spp.	0.6	0.2	0.1	0.1
Marine worm: class Polychaete	8.0	2.5	3.7	2.0
Total		100	100	100
Samples (total)				
Scats containing identifiable prey (2760)				
Scats containing only unidentifiable prey (192)				
Empty scats (80)				
Total collected (3032)				

length ranges, the size of primary prey consumed by sea lions was assessed at a broad scale only. Detailed assessments of the size of some prey species consumed by Steller sea lions have been reported elsewhere and require the accurate measurement of selected cranial structures and the application of digestive correction factors (Tollit et al. 2004, Zeppelin et al. 2004) unavailable in our study.

Data analyses. Diet composition and the relative importance of each prey type were assessed using 3 standard indices expressed as percentages: frequency of occurrence (FO: proportion of scats with identifiable prey containing a given prey type), relative occurrence (RO: proportion of total occurrences of prey made up of each prey type), and relative abundance (RA: proportion of the total number of prey items made up of each prey type). Relative occurrence gives the same relative value as FO, but, unlike FO, sums to 100% and allows direct comparison between collections and other indices. We also calculated an index of importance (IIMP), which combines information on both occurrence and abundance. The percentage IIMP was calculated following García-Rodríguez & Aurióles-Gamboa (2004) as:

$$\text{IIMP}_j = 100 \times \left[\frac{1}{U} \sum_{j=1}^U \frac{X_{ij}}{X_j} \right]$$

where X_{ij} is the number of individuals (MNI) of prey type i in scat j , X_j is the total number of individuals from all prey found in scat j , and U is the total number of scats in the sample with identifiable prey. Although the importance of each prey type in diet studies is best represented by volumetric data (Hyslop 1980), biomass contribution was not calculated in the present study due to the subjective method of size classification employed and lack of species-specific numerical correction factors.

Diet diversity was estimated for each collection using the Shannon's index of diversity, H' , based on frequency of occurrence. To compare diversity on a linear scale, the exponential of the Shannon entropy value was calculated to give the effective number of species (ENS: the number of equally common species required to give a particular value of the diversity index; MacArthur 1965). To compare diet diversity with previous Steller sea lion dietary studies, prey were grouped into 7 categories following Merrick et al. (1997): gadids, salmon, forage fish, hexagrammids, flat fish, cephalopods, and others. Shannon's index of diversity was then calculated using the split-sample frequency of occurrence (SSFO) following Merrick et al. (1997). The exponential of the Shannon entropy value, referred to by Merrick et al. (1997) as the diet diversity index (DDI), ranges from 1 (1 prey group in the diet) to 7 (all 7 prey groups). To compare our esti-

mates of DDI with those for southeast Alaska in the 1990s, seasonal DDI values were calculated from the SSFO data presented for the 7 prey categories in Winship & Trites (2003).

The similarity or overlap in diet composition among regional and seasonal collections was quantified using the Bray-Curtis coefficient of similarity (S) (Bray & Curtis 1957). The value of S ranges from 0 to 1; $S = 0$ indicates no overlap in prey use and $S = 1$ indicates perfect overlap in prey use. Two collections were considered relatively similar for $S \geq 60\%$, based on examination of multi-dimensional scaling (MDS) plots and dendograms of collections (PRIMER v. 5). An MDS stress factor of <0.2 was assumed to indicate that the MDS plot was an accurate representation of the relationships between collections (Schiffman et al. 1981). Rare species were not removed from analysis, as the similarity measure used automatically down-weighted the contribution of less common species.

Cumulative prey curves were constructed to evaluate the adequacy of sample sizes to represent diet composition. Each was constructed using randomization procedures (EstimateS v. 8) based on the occurrence of primary prey. To reduce the influence of exceptionally rare or secondarily consumed species, prey that occurred in $\leq 5\%$ of samples in any one collection were excluded. Sample-based curves were plotted by calculating the means of the number of prey identified, following repeated re-sampling of scats without replacement and 100 randomizations of scat order. Sampling adequacy was evaluated by visual inspection of curve stabilization. Prey accumulation curves were calculated for each season within the 4 regions using collections pooled across years.

Statistical analysis. The relative rank of prey types were compared between indices of importance using the Spearman's rank correlation coefficient (r_s), and the Mann-Whitney U -test was used to test for significant differences in H' among seasons and regions (SPSS v. 13.0). Mean values are given (\pm SD). Overall differences in diet between regions and between seasons within each region were statistically tested using nonparametric analysis of similarities (ANOSIM) on the Bray-Curtis similarities matrices (PRIMER v. 5) and 999 randomizations of collections. ANOSIM tests the null hypothesis that within-group similarities do not exceed between-group similarities. This test has a number of advantages over univariate tests and does not assume variability of within-group replications is similar for all groups. Where significant differences between groups were found, pair-wise tests were used to identify the main differences. Due to a limited number of collections (replicates) in some comparisons the value of the test statistic R was used to assess between-group differences, where mid- to high-range values of

R are indicative of complete separation of groups and values close to zero imply little or no difference (Clarke & Warwick 2001). All other statistical analysis used a significance level of $\alpha = 0.05$. The main species contributing to the observed differences were determined based on their relative contribution to the average Bray-Curtis dissimilarity between groups, using similarity of percentage (SIMPER) analysis (PRIMER v. 5). Only species contributing to $\geq 10\%$ of the observed dissimilarity between groups are listed. Only collections where > 1 region was sampled for a given year and season were included in analysis of similarity. Due to the limited number of collections available for the southern region, ANOSIM was restricted to comparisons among north, east, and west collections, unless stated otherwise. Analysis performed using IIMP did not alter general conclusions, although the rank of discriminating prey varied slightly. Only statistical analyses based on RO are presented here.

RESULTS

Sample distribution

A total of 2760 scats containing identifiable prey remains were collected from September 1999 through March 2005 (Table 1). Scat collection was affected by seasonal changes in Steller sea lion *Eumetopias jubatus* distribution and haulout accessibility. As a consequence, the size and number of collections were variable across sites, seasons, and years. Most scats were collected from sites in the north (44.4%), east (29.2%), and west (19.1%), whereas the number of scats from the south was small (7.2%) and limited to summer and fall. Collections were largely biased towards the non-breeding season, with summer collections contributing to only 18.2% of the total number of scats. Scats collected in summer were primarily from the north (51.7%) and south (26.5%). Overall, 87.9% of scats were collected between 2000 and 2003, with seasonal collections incomplete in 1999, 2004, and 2005.

Summary of diet composition

In total, 76 prey types were identified: 48 to species level, 11 to genus, 13 to family, 1 to class, 2 to order and 1 to group (Table 2). Fish remains were found in all scats with identifiable prey: cephalopods in 5.4%, and polychaete worms in 8.0%. Crustacean remains consisting of carapace fragments of crabs, isopods, and euphausiids were noted in a large number of scats, but were not included in analysis due to difficulties in enu-

meration, advanced degradation, and variable effort in identification over the study period. Overall, unidentified fish were recorded in 3% of scats and ranged from 0 to 9% among collections.

When samples were pooled across years, seasons, and regions, 9 main prey types were identified with FO $\geq 10\%$ (Table 2). Pacific sand lance *Ammodytes hexapterus* (hereafter referred to as sand lance), walleye pollock *Theragra chalcogramma* (hereafter referred to as pollock) and arrowtooth flounder *Atheresthes stomias* were the most common prey, occurring in 35 to 42% of all scats. Pacific cod *Gadus macrocephalus*, salmon *Oncorhynchus* spp. and Pacific herring *Clupea pallasii* (hereafter referred to as herring) occurred in 23 to 32% of scats, and Irish lords *Hemilepidotus* spp., Pacific sandfish *Trichodon trichodon*, and unidentified gadids (family Gadidae) occurred in 10 to 11% of scats. Based on a minimum number of 8730 individual prey identified, the most numerically abundant prey was sand lance (39%), followed by pollock (11%), capelin (8%), herring (6%), arrowtooth flounder (6%), and Pacific cod (6%) (Table 2). On average, sand lance and capelin were the most abundant prey per scat when present (Table 3). The mean number of prey types identified per scat was 3.2 ± 2.1 and ranged from 1 to 19 prey types. Of the scats containing a single identifiable prey ($n = 622$), most contained pollock (20.7%), arrowtooth flounder (19.5%), or salmon (12.4%). Sand lance was the prey most frequently co-occurring in scats containing Pacific cod (61.5%), salmon (60.2%), herring (50.9%), and pollock (50.0%). In scats containing arrowtooth flounder, sand lance and pollock co-occurred in similar proportions (47.8 and 47.2%, respectively).

The relative importance of each prey type based on the 3 indices (RO, RA, and IIMP) was similar, with only a few principle discrepancies (Table 3). Capelin was ranked as the third most important prey based on relative abundance, but only the tenth in regard to their occurrence. In terms of IIMP, capelin was ranked seventh, indicating that although capelin occurred less frequently than other main prey, they consistently occurred in relatively high abundance when present in scats. Polychaete worms were also ranked higher in importance based on abundance compared to occurrence. However, examination of the distribution of MNI indicated that RA was dominated by 2 scats containing 106 and 133 individuals, whereas most scats in which polychaetes were present contained 1 to 3 individuals. Thus, their overall ranking based on IIMP was much lower and similar to that based on RO. Irish lords were also ranked slightly lower in terms of RA and IIMP compared to RO, reflecting that although common, most samples (90%) contained only 1 individual. Although IIMP was highly correlated with both

RO ($r_s = 0.980$, $p = 0.000$, $n = 24$) and RA ($r_s = 0.964$, $p = 0.000$, $n = 24$), the stronger relationship with RO reflected the greater influence of occurrence on IIMP and down-weighting of individual scats with unusually high abundances of a given prey.

Sand lance recovered from scats were estimated to range in size from <7 to 27 cm FL and were grouped into 3 size categories: ≤7 cm (small), 8 to 19 cm (medium), and 20 to 27 cm (large). Of scats, 83% contained medium-sized sand lance, 22% large sand lance, and 20% small sand lance. Pollock recovered in scats were estimated to range in length from <8 to 54 cm FL and were grouped into the 3 size and age classes: juvenile (≤20 cm), subadult (21 to 34 cm), and adult (≥35 cm) (Hughes & Hirschhorn 1979, DiCosimo & Kimball 2001). Overall, subadult pollock (60%) were the most dominant age class based on frequency of occurrence, followed by adult (37%) and juvenile (35%) pollock. Arrowtooth flounder ranged in size from <16 to 70 cm, with 91% of scats containing flounder estimated to be within the range of 25 to 59 cm. Pacific cod ranged in size from <8 to 69 cm FL, and most scats (94%) contained fish ≥27 cm, with 69% of scats containing cod within the 50 to 69 cm range. Salmon in scats were estimated to range in length from <15 to 90 cm, with a major peak in size distribution at

30 to 59 cm and a smaller peak at 16 to 29 cm. Capelin ranged in size from <5 to 18 cm FL, with 94% of scats containing capelin 10 to 18 cm in length. Herring ranged in size from <8 to 35 cm FL, with most scats (97%) containing herring 11 to 35 cm in length.

Cumulative prey curves indicated that the relative increase in the number of new prey identified per additional scat was small (<2%) following examination of 23 scats (Fig. 2). To reduce biases in diet composition due to small sample size, while retaining a sufficient number of collections for spatial and temporal comparisons, collections with <23 scats were excluded from further analysis. This size was considered sufficient to describe the relative contribution of the main prey species to the Steller sea lion diet. The mean sample size of scats retained in the analysis was 56.3 ± 36.1 , with most (70%) collections containing >35 scats.

Examination of individual collections suggested that species composition and relative importance of prey varied by region, season, and year (Figs. 3 & 4, Appendix 1, available as MEPS Supplementary Material at: www.int-res.com/articles/suppl/m360p265_app.pdf). A total of 24 prey occurred with ≥10% FO in any 1 collection (Table 3). Twelve prey had IIMP values ≥10% in any 1 collection (Table 3) and accounted for 78% of identifiable prey by occurrence and 90% by number.

Table 3. Primary prey (≥10% frequency of occurrence for any collection), ranked by percentage relative occurrence (RO), relative abundance (RA), and index of importance (IIMP). The minimum number of individuals (MNI) per scat when present is given as a mean and range. Values are for all 2760 scats pooled. Prey highlighted in bold had IIMP values ≥10% in any 1 collection. Primary habit(s) (P: pelagic; D: demersal; S: schooling) were assigned following Mecklenburg et al. (2002)

Prey type	Habit	RO	(Rank)	RA	(Rank)	IIMP	(Rank)	MNI per scat	
								Mean	Range
Pacific sand lance	PDS	13.2	(1)	38.6	(1)	16.1	(1)	7.1	1–394
Walleye pollock	PD	11.6	(2)	10.9	(2)	15.1	(2)	2.3	1–74
Arrowtooth flounder	D	11.0	(3)	5.6	(5)	12.5	(3)	1.2	1–7
Pacific cod	PDS	10.1	(4)	5.6	(5)	9.5	(4)	1.4	1–19
Pacific salmon	PD	8.3	(5)	4.3	(6)	8.4	(5)	1.3	1–11
Pacific herring	PS	7.3	(6)	6.3	(4)	7.7	(6)	2.1	1–44
Irish lord, unidentified	D	3.4	(7)	1.6	(10)	2.4	(10)	1.1	1–4
Pacific sandfish	D	3.3	(8)	2.8	(8)	2.5	(9)	2.1	1–34
Gadids, unidentified	PDS	3.3	(8)	1.8	(9)	3.3	(8)	1.3	1–29
Smelt, unidentified	P	2.8	(9)	1.3	(11)	2.1	(12)	1.1	1–3
Flatfish, unidentified	D	2.8	(9)	1.2	(12)	2.2	(11)	1.1	1–4
Capelin	PS	2.7	(10)	7.9	(3)	3.9	(7)	7.0	1–128
Polychaete worm	D	2.5	(11)	3.7	(7)	2.0	(13)	3.5	1–133
Rock sole	D	2.1	(12)	1.0	(14)	1.5	(15)	1.1	1–4
Snailfishes, unidentified	D	2.0	(13)	1.1	(13)	1.8	(14)	1.4	1–8
Skates	D	1.5	(14)	0.6	(15)	1.0	(16)	1.0	1
Sculpins, unidentified	D	1.2	(15)	0.5	(16)	0.8	(18)	1.1	1–2
Rockfish	D	1.1	(16)	0.5	(16)	0.7	(19)	1.0	1
Pacific halibut	D	0.9	(17)	0.4	(15)	0.9	(17)	1.1	1–2
<i>Hexagrammos</i> spp.	D	0.8	(18)	0.5	(16)	0.5	(20)	1.6	1–16
Gunnel, unidentified	D	0.6	(19)	0.3	(14)	0.3	(21)	1.2	1–3
Lumpsucker, unidentified	PD	0.4	(20)	0.2	(13)	0.3	(21)	1.0	1
Eulachon	P	0.3	(21)	0.2	(13)	0.2	(20)	1.3	1–2
Smooth lumpsucker	PD	0.1	(22)	0.1	(12)	0.1	(19)	1.5	1–4

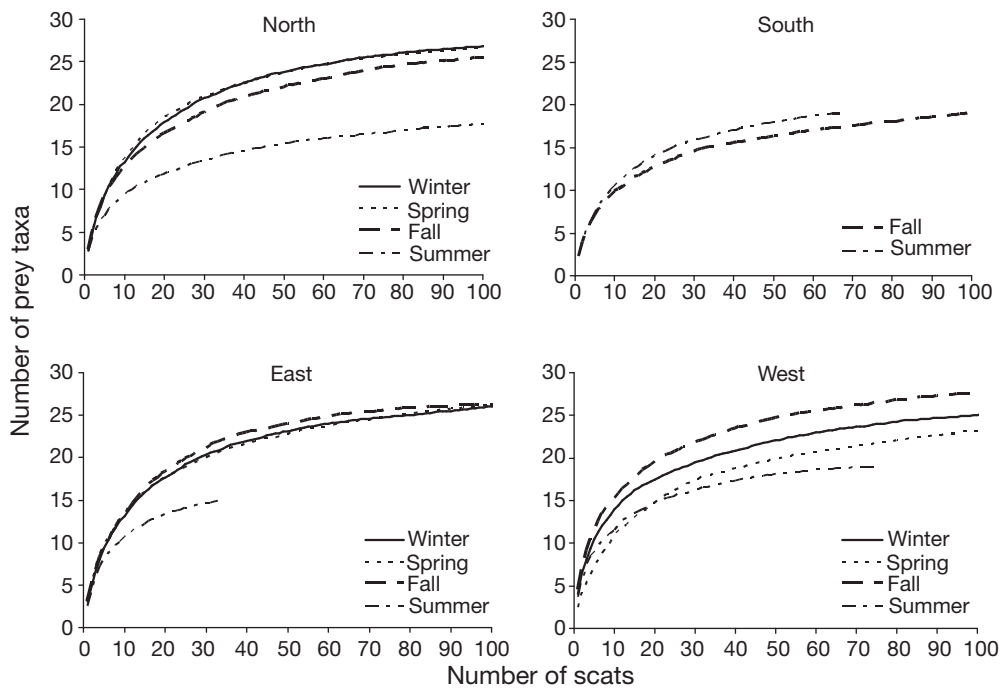


Fig. 2. Cumulative curves of the mean number of prey types identified in Steller sea lion scats collected in 4 regions of the Kodiak Archipelago (1999 to 2005). Cumulative curves were constructed using randomization procedures (100 times), without replacement

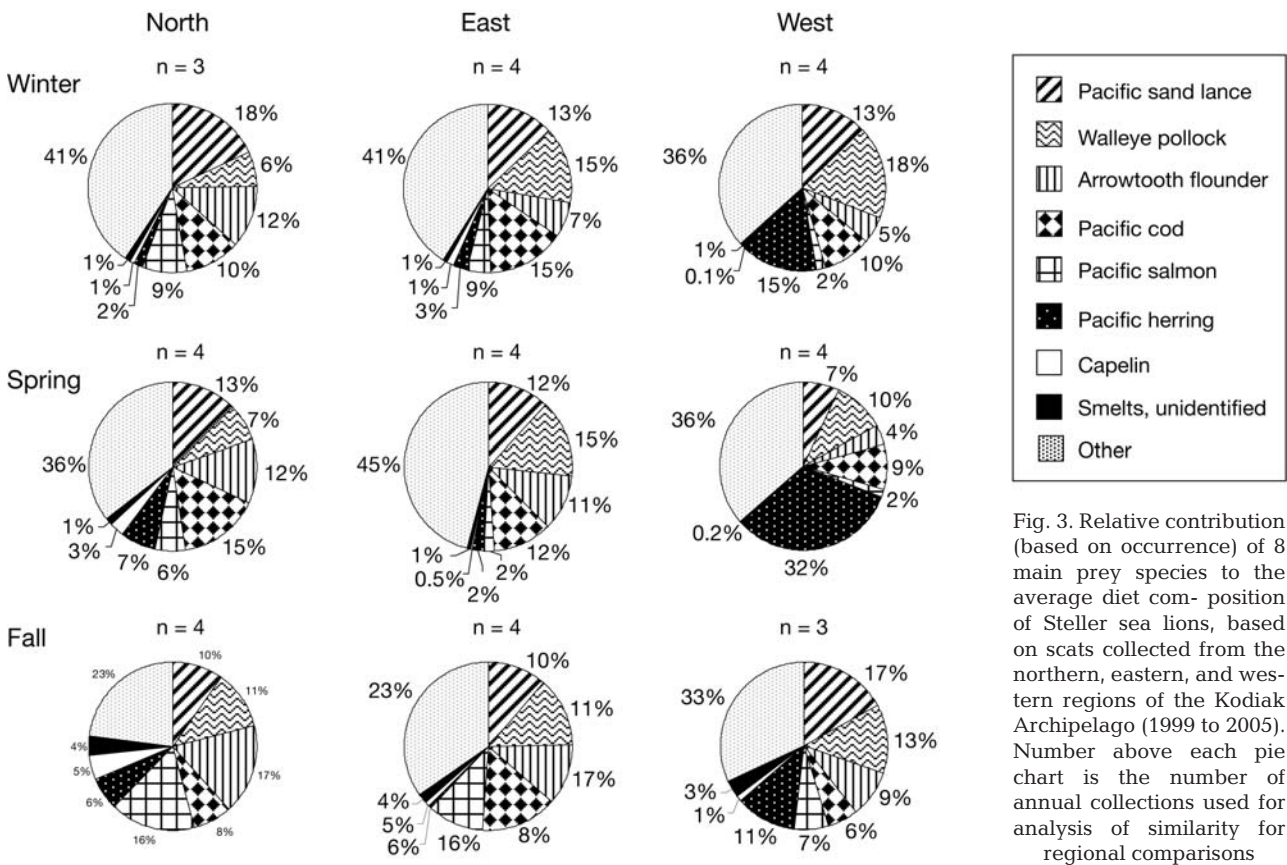


Fig. 3. Relative contribution (based on occurrence) of 8 main prey species to the average diet composition of Steller sea lions, based on scats collected from the northern, eastern, and western regions of the Kodiak Archipelago (1999 to 2005). Number above each pie chart is the number of annual collections used for analysis of similarity for regional comparisons

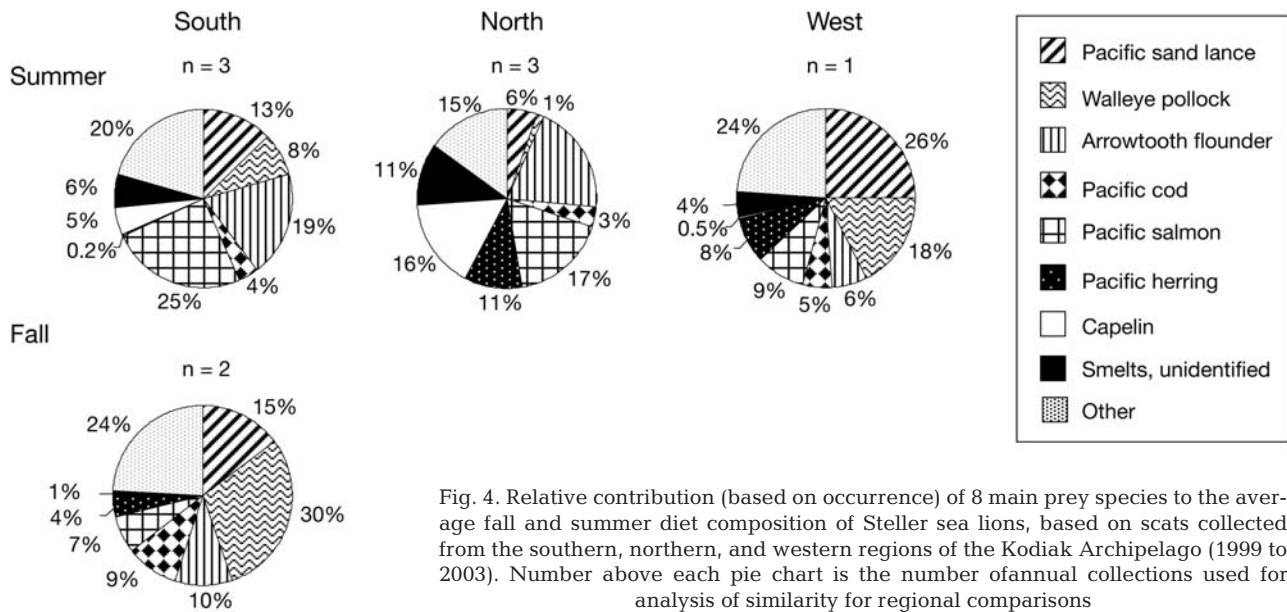


Fig. 4. Relative contribution (based on occurrence) of 8 main prey species to the average fall and summer diet composition of Steller sea lions, based on scats collected from the southern, northern, and western regions of the Kodiak Archipelago (1999 to 2003). Number above each pie chart is the number of annual collections used for analysis of similarity for regional comparisons

Regional variation in diet composition

Using the Bray-Curtis similarity matrices based on the relative occurrence of prey, differences in diet composition among regions were significant within each season (Table 4, Figs. 3 & 4). In winter, diet composition was similar between collections from the north and east (mean $S = 64.5\%$; $R = 0.20$, $p = 0.114$), but significantly different between the west and north (mean $S = 53.7\%$; $R = 0.87$, $p = 0.029$), and west and east (mean $S = 61.3\%$; $R = 0.45$, $p = 0.029$; Fig. 3). The most common prey in all 3 regions in winter were sand lance, pollock, Pacific cod, and arrowtooth flounder, although they occurred in different proportions among regions and years (Fig. 3, Appendix 1A, B, C). Differences in winter diet among regions were largely attributed to the relatively high occurrence of herring in the west (accounting for 14 and 16% of the difference between north and east, respectively) and a relatively low occurrence of pollock in the north compared to the west (12% of the difference).

As in winter, spring diet composition was similar in the north and east (mean $S = 61.5\%$; $R = 0.18$, $p = 0.143$), but differed significantly between north and west (mean $S = 47.0\%$; $R = 0.98$, $p = 0.029$) and east and west (mean $S = 49.6\%$; $R = 0.99$, $p = 0.029$; Fig. 3). The most common prey among the 3 regions in spring were similar to winter (Fig. 3). Differences in spring diet composition between regions were largely due to a relatively high occurrence of herring in the west compared to in the north and east (24 and 30% of the difference, respectively; Fig. 3).

In fall, only the composition of east and west diets differed significantly (mean $S = 57.7\%$; $R = 0.61$, $p = 0.029$); diet composition in the north was similar to that in the west (mean $S = 58.9\%$; $R = 0.24$, $p = 0.143$) and east (mean $S = 61.7\%$; $R = 0.04$, $p = 0.286$). The most common prey in all 3 regions in fall were pollock, arrowtooth flounder, sand lance, and salmon, although they occurred in different proportions among regions and years (Fig. 3, Appendix 1A, B, C). Variation in diet between east and west was largely attributed to a relatively higher occurrence of herring (13% of difference) and sand lance (11% of difference) in the west, and a higher occurrence of Pacific cod in the east (11% of difference). Although the average diet composition in the north appeared to be different from that in the east and west (Fig. 3), inter-annual variation in fall diet in the north was greater than the differences between regions (Table 5). Limited fall collections in the south precluded statistical analysis using ANOSIM, but overlap in diet between the south and all other regions was low

Table 4. Analysis of similarity of diet composition of Steller sea lion scat collections within and among regions and seasons. The numbers of collections used in each analysis are listed (n)

Comparison	Season/location	Location/season	Global R	p	n
Regional	Winter	North, East, West	0.503	0.004	11
	Spring	North, East, West	0.762	0.003	12
	Fall	North, East, West	0.243	0.028	11
Seasonal	Summer	North, South	0.444	0.100	6
	North	All	0.496	0.004	16
	East	Excludes summer	0.03	0.287	14
	West	Excludes summer	0.73	0.001	11

Table 5. Bray-Curtis overlap (similarity) indices matrix for the diet composition of Steller sea lion scat collections among regions and years within each season. Numbers in bold indicate low similarity in diet ($S < 60\%$). Solid boxes highlight annual similarity within each region and dashed boxes highlight between-region similarities

Winter	North 00	North 01	North 02	East 00	East 01	East 02	East 03	East 04	West 00	West 01	West 02			
North 01	76.6													
North 02	60.5	72.1												
East 00	78.2	74.2	61.4											
East 01	72.0	72.8	58.1	78.5										
East 02	79.7	70.6	55.8	80.7	71.9									
East 03	65.3	58.4	45.5	72.0	70.9	70.8								
East 04	53.3	51.9	46.4	58.8	61.2	52.0	63.5							
West 00	66.1	57.0	53.0	70.4	67.2	70.7	64.8	53.6						
West 01	58.6	53.0	47.1	65.1	63.4	63.1	67.4	56.7	75.5					
West 02	44.5	37.7	40.2	50.9	50.7	56.5	56.8	41.6	67.6	64.6				
West 04	65.0	65.7	55.9	73.6	71.3	67.2	59.4	58.7	75.4	73.2	65.8			
Spring	North 00	North 01	North 02	North 03	East 00	East 02	East 03	East 05	West 01	West 02	West 03			
North 01	58.2													
North 02	53.0	70.2												
North 03	64.2	57.6	70.2											
East 00	56.6	68.4	70.6	58.2										
East 02	43.9	52.3	60.7	56.4	65.4									
East 03	54.4	59.8	75.7	67.2	70.8	64.3								
East 05	58.4	71.9	69.3	60.7	79.3	57.6	64.2							
West 01	52.9	45.4	50.2	52.6	53.3	59.7	46.2	57.5						
West 02	50.6	36.6	48.5	47.3	50.4	49.6	47.5	46.6	62.5					
West 03	45.7	30.6	40.2	44.7	43.8	48.2	41.7	39.7	62.3	77.0				
West 05	52.9	42.5	53.4	57.5	52.3	54.8	50.6	51.7	73.6	72.0	75.6			
Fall	North 99	North 00	North 01	North 02	North 04	East 99	East 00	East 01	East 02	East 03	West 99	West 01	West 02	South 99
North 00	53.5													
North 01	58.1	65.8												
North 02	54.7	64.3	76.4											
North 04	62.3	55.6	58.3	58.4										
East 99	51.0	72.1	65.0	69.8	60.0									
East 00	47.9	62.9	71.6	78.0	57.4	64.3								
East 01	41.6	53.8	61.0	70.9	47.7	59.5	69.2							
East 02	48.5	54.8	63.2	74.6	52.2	60.8	65.6	65.6						
East 03	42.8	47.3	48.0	51.0	36.0	41.1	47.4	55.4	49.5					
West 99	44.1	52.6	66.3	60.0	50.1	49.5	61.6	53.2	49.0	40.2				
West 01	49.5	54.8	73.8	69.8	50.2	58.5	72.3	61.3	56.0	42.5	68.6			
West 02	55.7	52.8	65.3	61.9	49.3	54.3	58.1	61.9	57.0	58.1	56.3	62.4		
South 99	50.2	58.1	68.2	59.3	56.1	58.2	58.4	50.4	51.3	34.4	72.8	60.9	52.6	
South 02	29.3	36.5	39.2	53.6	25.0	40.0	45.9	56.5	54.5	75.4	33.8	42.9	49.0	29.5
Summer	North 00	North 01	North 02	North 03	South 00	South 01	South 03							
North 01	56.1													
North 02	65.2	59.5												
North 03	59.9	71.5	74.9											
South 00	47.8	56.1	42.9	47.8										
South 01	40.6	36.8	55.5	51.0	42.3									
South 03	53.1	64.2	57.2	67.0	61.9	56.5								
West 02	42.9	42.1	47.1	43.4	55.4	50.1	46.8							

(mean $S = 47.5$ to 52.5% ; Table 5). Differences in diet were largely attributed to the dominance of pollock (22 to 24% of difference) and low proportion of salmon (7 to 10% of difference) in the south compared to the north, east, and west (Figs. 3 & 4).

Regional comparisons of summer diet were limited (Fig. 4). Diet composition averaged over 3 yr (2000, 2001, and 2003) differed significantly between north and south with a mid-range value of R of 0.44 (mean $S = 51.6\%$; $p = 0.1$; Table 4). The most common summer prey in these 2 regions were arrowtooth flounder, salmon, smelts (including capelin), and sand lance (Fig. 4). Differences in diet composition between regions were mostly attributed to a high occurrence of salmon (17% of difference) in the south and a relatively high occurrence of capelin and herring in the north (12 and 11% of the difference, respectively). Overlap in diet between north and west in summer 2002 was also low ($S = 47.1\%$), and attributed to 4 prey species (salmon with 19%, pollock with 15%, sand lance with 14%, and capelin with 12% of the difference).

Seasonal variation in diet composition

Seasonal variation in diet composition within regions was significant for collections in the north and west, but not in the east (Table 4). In the north, significant differences in diet occurred between summer and all other seasons (mean $S = 41.8$ to 56.5% ; $R = 0.51$ to 1, all $p < 0.05$), with 5 prey types contributing to $\geq 10\%$ of observed differences in diet in at least 1 pair-wise seasonal comparison. Together, 23 to 27% of the difference in diets was attributed to the relatively high occurrence of capelin and salmon in summer. A relatively low occurrence of Pacific cod in summer attributed a further 11% to the difference between summer and spring, and a high occurrence of arrowtooth flounder in fall attributed 13%. Sand lance was also more important in winter (10% of difference) compared to in summer.

In the west, significant differences in diet composition were found between spring and both winter and fall (mean $S = 59.3\%$; $R = 0.90$ and mean $S = 54.2\%$; $R = 0.94$, respectively; both pair-wise $p = 0.029$), and were largely (21 to 23%) attributed to an over 2-fold increase in the occurrence of herring in spring. A relatively low occurrence of sand lance in spring compared to fall and a high occurrence of pollock in winter compared to spring explained a further 10 to 12% of seasonal differences. In the east, no significant differences were found in diet composition between seasons, given the diet collections available (Table 4).

Annual variation in diet composition

Variation in diet composition between years was evident within all seasons and regions (Table 5). In general, interannual overlap in diet was lowest among spring and fall collections, whereas collections from the north and east generally displayed the greatest interannual variation in prey composition. Interannual differences in the diet in spring and fall were largely ($\geq 10\%$ of differences among years) attributed to variation in the relative occurrence of the most dominant prey: in spring, Pacific cod, arrowtooth flounder, and pollock and, in fall, arrowtooth flounder, salmon, pollock, and sand lance (Appendix 1).

The most marked interannual change in diet over the study period was the unusually high occurrence of pollock in fall 2003 in the east ($RO = 54\%$), which alone accounted for most (37 to 42%) of the interannual differences in diet. In 2003, the occurrences of Pacific cod ($RO = 6\%$) and sand lance ($RO = 2\%$) were also relatively low in fall compared to other years, and, together with pollock, explained 53 to 64% of the difference in diet among years in the east. Variation in the occurrence of these 3 species was also mirrored by changes in their relative abundance, suggesting their contribution to differences in diet composition in terms of biomass was significant. In contrast to the east, the occurrence of pollock in fall was unusually high in 2002 in the south ($RO = 53\%$) and west ($RO = 21\%$), whereas, in the north, it remained similar to previous years ($RO = 13\%$), but was unusually low in 2004 ($RO = 2\%$). Assessment of regional fluctuations in the occurrence of cod was limited due to the absence of data from fall 2003 in the north, south, and west.

Annual variation in the occurrence of lower ranked prey such as herring and capelin also contributed considerably to differences in diet among years. For example, during spring in the north, a large proportion (12 to 20%) of annual diet variation was attributed to herring, the occurrence of which was relatively high in 2000 ($RO = 17\%$) and 2003 ($RO = 10\%$), but absent from scats in 2001 and low in 2002 ($RO = 2\%$). A gradual decline in the occurrence of capelin in the north over the study period explained $\geq 10\%$ of differences in diet among years in both spring and fall. In the east, an unusually high occurrence ($RO = 21\%$) of Pacific sandfish in 2002 accounted for up to 23% of annual differences in diet.

Diet diversity

Diet diversity averaged over all collections was 2.50 ± 0.31 using the Shannon index H' ($ENS = 12$) and 4.30 ± 0.82 using Merrick's DDI for 7 prey groups.

Within each season, diet diversity was similar between regions (all pair-wise U -tests, $p > 0.05$), although spring diversity in the west ($H' = 2.34 \pm 0.23$) was slightly lower and approached a significant difference compared to the diet in the north and east (2.71 ± 0.19 and 2.68 ± 0.05 , respectively; both pair-wise comparisons, $p = 0.08$). Averaged across all regions, diet diversity differed significantly between summer and all other seasons (all pair-wise U -tests, $p < 0.05$), but was similar between winter, spring, and fall (all pair-wise U -tests, $p > 0.1$); diversity was lowest in summer ($H' = 2.22 \pm 0.25$, ENS = 9) and highest in winter (2.67 ± 0.16 , ENS = 14), spring (2.58 ± 0.23 , ENS = 13), and fall (2.45 ± 0.38 , ENS = 12). Comparisons between annual collections in the non-breeding season indicated that diet diversity in 2001 (2.78 ± 0.10) was higher than in 2002 (2.48 ± 0.56 ; $U = 15.500$, $p = 0.029$) and 2003 (2.38 ± 0.42 ; $U = 4.000$, $p = 0.018$), but not significantly different from 2000 (2.68 ± 0.19 ; $U = 21.500$, $p = 0.449$). In contrast, diet diversity in summer (breeding season) was lowest in 2001 (1.87 ± 0.31), compared to 2000, 2002, and 2003 (2.38 ± 0.03 , 2.33 ± 0.07 , 2.28 ± 0.04 , respectively). Analysis of DDIs identified similar patterns.

DISCUSSION

Steller sea lion diet in Kodiak Archipelago

In concordance with previous studies, the prey identified in the present study indicate that Steller sea lions *Eumetopias jubatus* are adept at foraging on a variety of prey including demersal, semi-demersal, and pelagic prey (Sinclair & Zeppelin 2002, Brown et al. 2002, Waite & Burkanov 2006, Trites et al. 2007b). The size range of prey consumed by sea lions was also wide, with prey up to ~70 cm FL taken. Compared to previous studies in Alaska our study reports a far greater number of prey species, although the main prey identified were similar. Of the 76 prey types identified in the present study, 24 occurred with $\geq 10\%$ FO in any 1 collection (Table 3). The 6 most dominant species across all collections, in order of overall occurrence, were sand lance, pollock, arrowtooth flounder, Pacific cod, salmon, and herring. However, there were significant differences in their proportional contribution among geographical regions, seasons, and years.

Over the study period (1999 to 2005) the diet averaged over all 4 seasons was dominated by herring, pollock, and sand lance in the west and arrowtooth flounder, sand lance, and salmon in the north. In the east, the non-summer diet (fall to spring) was dominated by pollock, Pacific cod, and sand lance, whereas

the diet in the south was dominated by salmon, pollock, and arrowtooth flounder, over summer to fall. Within each season, diets were most similar between adjacent regions (Fig. 1); diets on the north and east side of Kodiak were relatively similar, whereas the diet on the western side of Kodiak differed markedly from all other regions. Seasonal collections in the south were too limited to establish the degree of diet overlap with the eastern region, but summer diets in the south differed from those in the north.

Regional and temporal differences in diet composition were largely attributed to variation in the relative occurrence of the main prey species. However, lower ranking prey such as capelin and Pacific sandfish increased in importance in some years. Within each region and season the ranking of the 3 to 4 dominant prey generally varied from year to year. The exceptions were winter collections in the north, which were consistently dominated by sand lance, and spring collections in the west, which were consistently dominated by herring. Even in summer, when diet diversity was low and largely dominated by a single species, the dominant prey species varied from year to year. In years when salmon dominated the summer diet in the north, arrowtooth flounder was dominant in the south and vice versa, except in 2000, when capelin dominated the diet in the north and arrowtooth flounder and sand lance occurred in similar proportions (26 and 22%, respectively) in the south.

In general, seasonal patterns in occurrence of prey such as herring, salmon, and capelin reflected expected changes in availability of prey due to fish life-history stages. Herring and capelin typically increased in the diet in spring and summer, respectively, when spawning fish aggregate in bays in dense schools (Blackburn et al. 1981, Brown 2002). Similarly, the occurrence of salmon increased in summer and fall with the inshore migration of prespawning salmon (Groot & Margolis 1991). The seasonal presence of arrowtooth flounder was variable among sites, but appeared to be lowest in winter and higher in summer. Pollock and sand lance were generally lowest over summer and highest in fall and winter, whereas cod was highest in winter and spring. However, without detailed information on the concurrent availability of prey, it is difficult to differentiate between changes that reflect seasonal availability of prey and changes that occur due to a decline in the availability of more preferred prey.

Spatial differences in the diet of sea lions most likely reflect the influence of local oceanographic and habitat features on the spatial distribution, composition, and abundance of fish communities (Robards et al. 1999a). Unfortunately there is limited information on the availability of most sea lion prey species. Most information

currently available is based on commercial fisheries catch data and stock assessment surveys, which provide only a broad snapshot of prey availability during a limited time period and are not designed to target sea lion prey or areas in which they forage. Although a number of studies have attempted to determine the fine-scale availability of Steller sea lion prey in the vicinity of rookeries and haulouts (e.g. Mueter & Norcross 2000b, Womble & Sigler 2006), most data are limited in spatial scale or species sampled and confounded by the fact that little is still known of the foraging distribution of Steller sea lions.

The greatest difference between the diet of Steller sea lions in the different regions was the relatively high occurrence of herring in scats from the western side of Kodiak. Herring are found seasonally in all bays around Kodiak, but occur in substantially higher spawning biomass along the west coast of Kodiak and Afognak Islands (Gretsch 2004). Uganik Bay currently supports the largest and most consistent spring spawning stock of herring in the Kodiak area (Gretsch 2004) and is approximately 15 km north of Cape Ugat (Fig. 1), the haulout where west Kodiak scats were collected. The occurrence of herring in the diet of sea lions using Cape Ugat was highest during spring, corresponding to the dense aggregation of spawning fish in bays along the west coast. Herring abundance was also relatively high in winter and fall, reflecting the large aggregations of overwintering herring in the eastern Shelikof Strait and adjacent bays (Gretsch 2004). Aerial counts of sea lions conducted between 1999 and 2003 also indicated that Cape Ugat was used throughout the year by a large number of sea lions, with a marked increase in numbers over the herring prespawning and spawning period (March and April) (Wynne 2005). In contrast, sea lion numbers at Cape Ugat dropped over summer, most likely reflecting the movement of animals to breeding colonies on the east coast of Kodiak and possibly the movement of some animals to other areas of predictable or seasonally abundant prey. Low counts in summer at Cape Ugat have generally corresponded to seasonal peaks in sea lion numbers at Chief Cove, ~20 km south of Cape Ugat, where sea lions have been observed to prey on salmon at setnet sites (Wynne 2005).

Given their extremely high energy content (Anthony et al. 2000) and local abundance, herring most likely provide an important seasonally predictable and energy-rich prey source in the nonbreeding season. Overwintering and spawning herring have also been noted as important prey for sea lions at a number of locations in southeast Alaska, where their distribution has been shown to influence the spatial distribution and abundance of Steller sea lions (Womble et al. 2005, Womble & Sigler 2006). Fine-scale analysis of the

spatial and temporal patterns in the diet of Steller sea lions in relation to trends in their use of terrestrial haulouts would greatly improve our understanding of the foraging behavior of this species and may assist in assessing what proportions of the population are utilizing particular prey resources.

Sand lance were a key prey item during all seasons for Steller sea lions throughout the Kodiak Archipelago and, like herring, are high in lipid content (Anthony et al. 2000). Sand lance are a small, semi-demersal, schooling species, commonly found in shallow near-shore habitats, where they burrow in fine gravel or sand substrates during darker periods, and forage diurnally in pelagic waters in densely aggregated schools close to their benthic refuge or further offshore (Robards et al. 1999b, Blackburn & Anderson 1997). Sand lance are an important energy-rich forage fish for many piscivorous predators, and changes in their abundance can significantly affect the population dynamics of many species (see review by Wilson et al. 1999). Unlike herring, sand lance are thought to be less restricted by water temperatures and able to occupy a wider range of habitats (Abookire & Piatt 2005), which may explain the relatively consistent contribution of sand lance to regional diets.

In the Kodiak area, pollock are broadly distributed over the outershelf and slope regions to shallower nearshore waters where it appears to be the most dominant demersal species (Mueter & Norcross 2000a, Jackson 2006). However, the abundance and size of pollock in the nearshore waters of Kodiak vary spatially and seasonally, with marked interannual variations in abundance (Anderson & Piatt 1999, Jackson 2006, Lowen 2007). Pollock biomass in nearshore waters typically declines in late winter with the migration of adults to offshore spawning areas in Shelikof Strait and gullies on the northeast side of Kodiak (Bailey et al. 1999, Wilson et al. 2005) and begins to increase again in late spring, with maximum biomass occurring in summer (Lowen 2007). In contrast, the occurrence of pollock in the diet of Steller sea lions at haulouts in the north and south was relatively low in summer compared to other seasons, suggesting a preference by sea lions for more energy-rich or accessible prey, such as salmon and capelin.

Interestingly, of the small forage fish captured in shrimp surveys in the Kodiak region in recent years, eulachon was the most abundant, over herring or capelin (Anderson & Piatt 1999, Jackson 2006). However, eulachon were only recovered in 15% of all collections ($n = 47$) between 1999 and 2005, and, when present, typically occurred at low frequencies (<9% FO). Eulachon have one of the highest energy densities of any forage fish in the North Pacific, second only to northern lampfish *Thaleichthys pacificus* and

markedly higher than herring and sand lance (Anthony et al. 2000). In some areas of southeast Alaska, prespawning aggregations of eulachon in spring are thought to be an important seasonal energy source for sea lions (Sigler et al. 2004, Womble et al. 2005). Eulachon spawning runs have been reported on the eastern side of Kodiak Island in the past (Blackburn et al. 1981), but are not known to concentrate in bays in the densities observed in southeast Alaska nor to attract large numbers of sea lions. When caught in survey trawls in bays around Kodiak, they generally occur in deeper water mixed with adult pollock (R. Foy unpubl. data). Therefore, although eulachon are far greater in energy content than herring or sand lance and, in some years, may occur in greater abundance, the energetic cost of foraging on a more dispersed prey at depths may outweigh the energetic benefit when alternative prey are available.

Detailed analysis of interannual trends in diet was limited due to variable sampling distributions among years and regions. However, there appeared to be an overall shift in the occurrence of some prey species over the study period, with an increase in pollock following 2002 and concurrent decline in sand lance and cod. These changes were more evident in the east than in other regions. An apparent decline in the catch per unit effort of Pacific cod from 2000 to 2005 was also noted in analysis of small-mesh shrimp surveys conducted in the Kodiak area (Litzow 2006). Interannual shifts in the contribution of capelin and sand lance to the diet of black-legged kittiwakes foraging on the east coast of Kodiak were also recorded, with a decline in sand lance and concurrent increase in capelin between 2001 and 2003 (Kildaw et al. 2005). At the time of analysis, results from concurrent Steller sea lion prey surveys on the northeast coast of Kodiak (R. Foy unpubl. data) were not available. However, future analysis of the fine-scale temporal and spatial availability of prey and oceanographic conditions over the study period will likely shed light on the factors influencing diet variability. To capture the range of variability in both sea lion diet and prey availability, it is important that future diet studies and assessment of prey availability or fisheries overlap are based on concurrent data collected over a number of years.

Potential biases

The data presented in our study provide the most comprehensive information available on diet composition of Steller sea lions in the Kodiak Archipelago and a measure of the spatial and temporal variation in prey consumed. Based on the prey accumulation curves, the samples retained in the analysis were considered suffi-

cient to describe the general diet composition and to assess spatial and seasonal variation in the importance of major prey species (Table 1, Fig. 2). However, additional seasonal collections are required to determine the extent of variation in diet between the south and other regions of Kodiak.

As with other methods of diet analysis, such as stomach content analysis, prey DNA and stable isotope ratios, the use of hard remains in scats to reconstruct diet is not without biases. The limitations and biases associated with scat analysis have been discussed previously for Steller sea lions (Cottrell & Trites 2002, Tollit et al. 2003, 2007, Joy et al. 2006) and other pinniped species (Dellinger & Trillmich 1988) and primarily relate to differential rates of digestion and recovery of diagnostic structures between and within prey species. Steller sea lion scats contain few otoliths, and erosion from partial digestion is high. Identification of all diagnostic skeletal structures in addition to otoliths, as used in our study, increases the detection rate of many species (Olesiuk et al. 1990, Cottrell & Trites 2002, Tollit et al. 2007). However, more robust bone structures from species such as pollock may have greater recovery rates compared to fragile structures of smaller species such as capelin and sand lance (Tollit et al. 2003, 2007). Therefore, the importance of small forage species may be underestimated in the present study. In addition, prey that leave no or few hard remains, or are preferentially regurgitated, such as cephalopods, will be underestimated (Tollit et al. 2007). In our study, only small cephalopod beaks and eye lenses were recovered from scats, but fragments of much larger beaks were sometimes found. The proportional contributions of other prey types, such as crustaceans, were also underrepresented because they left few identifiable remains and were difficult to enumerate. Prey recovered from scats are also thought to be biased towards prey consumed by seals just prior to hauling out and may not be representative of all prey consumed during a foraging trip. Crude passage rates for prey remains in captive Steller sea lions range from 2 to 3 d, although some prey may be retained for longer and deposited over a greater period of time (Tollit et al. 1997, 2007). Thus, the consumption of some prey species may be quantified more accurately than that of others. However, assuming that the biases remain relatively constant across collections, conclusions about differences in diet are still valid.

The relative importance of prey in the present study was based largely on frequency of occurrence and did not take into account differences in the number and size of prey consumed. However, the rank of particular prey based on frequency of occurrence was similar to that based on relative abundance and the composite index incorporating occurrence and abundance (IIMP).

Provided sample sizes are relatively large, FO indices can provide useful dietary information in the absence of biomass estimates (Olesiuk et al. 1990, Sinclair & Zeppelin 2002, Tollit et al. 2007). However, the limitations and biases associated with scat analysis and the indices used should be taken into consideration when interpreting our results.

Comparison with historical studies

Our study identified a similar suite of prey as those noted in previous studies conducted in the Kodiak area (Merrick et al. 1997, Sinclair & Zeppelin 2002). However, the dominance of the main prey differed markedly between studies. The most common prey identified in scats from the Kodiak region in the 1990s were pollock, arrowtooth flounder, salmon, and Pacific cod (Sinclair & Zeppelin 2002). Pollock was the most dominant prey in summer and winter collections in the 1990s, whereas the average summer and winter diets from 2000 to 2004 were dominated by sand lance and arrowtooth flounder, respectively. Sand lance, which was important in most collections in the early 2000s, occurred infrequently in the 1990s, with an overall frequency of occurrence of 9.5 and 17.7% in summer and winter, respectively (Sinclair & Zeppelin 2002). Small forage fish such as capelin and herring also appeared to be less important in the 1990s than in the present study.

Differences in the dominant prey in scat samples collected in the 1990s and early 2000s suggest that a temporal shift in diet composition may have occurred. Although some of the differences in proportional contribution of particular prey species are likely due to differences in sampling distributions between studies, the consistent dominance of pollock at individual sites sampled in the 1990s suggests an overall decline of the importance of pollock. Individual site collections in the 1990s were limited in sample size and pooled across variable years, which may introduce biases due to interannual variability in the consumption of pollock (present study) or strong recruitment years. However, the frequency of occurrence of pollock in the 1990s was consistently high among site samples, whereas sand lance was only ranked in the top 3 prey items at 1 site and occurred less frequently than pollock and Pacific cod (Sinclair & Zeppelin 2002). The size of pollock recovered from sea lion scats from the Bering Sea and Gulf of Alaska between 1998 and 2000 (mean FL = 39.3 cm; SD = 14.3) (Zeppelin et al. 2004) was also larger than that from Kodiak between 1999 and 2005 (primarily 21 to 34 cm). Although these size differences add weight to a temporal change in the contribution of pollock to the diet of sea lions, the degree of change

remains unclear due to differences between studies, in sampling distributions, and in the use of digestive correction factors.

In exploring the possible relationship between diet and population decline in Steller sea lions, it has been suggested that diet diversity in the 1990s was lowest where the sharpest declines in Steller sea lion populations occurred (Merrick et al. 1997, Trites et al. 2007b). Furthermore, it was suggested that diet diversity may be a proxy for the overall energy content of diet, with low diet diversity equating to low energy content (Winship & Trites 2003). In the Kodiak region in the early 2000s, diet diversity in summer (mean DDI = 3.9) was higher than reported in the 1990s for the Gulf of Alaska (DDI = 2.8; Merrick et al. 1997), but lower than calculated for southeast Alaska (DDI = 4.8; based on 7 prey categories, Trites et al. 2007b). Merrick et al. (1997) suggested that as diet diversity increased, the rate of population decline decreased; therefore, the higher diversity measured for Kodiak may reflect reduced rates of population decline between the 1990s and the period of this study (1999 to 2005). However, this trend was not demonstrated in diet studies conducted between 2000 and 2003 in Russian waters at the western extent of the population range, where some of the areas with the highest diversity also had the highest levels of population decline (Waite & Burkanov 2006).

In interpreting relationships between diet diversity and population trends it must also be emphasized that diet diversity is based only on the number of prey groups consumed and by itself does not reflect the biomass or energy content of individual prey species. For example, diet diversity in spring on the west side of Kodiak was low (mean H' = 2.3) compared to in other regions, but was dominated by energy-rich herring. As highlighted by Waite & Burkanov (2006), little can be inferred about the foraging success of populations from diet diversity measures without further information on prey availability and on the quality and quantity of prey consumed.

The diet composition and diversity derived from the analysis of scats collected from land may also be influenced by the age and sex structure of animals occupying the sites sampled. In our study, summer samples were collected mainly from haulouts with a mixed age and sex structure, whereas those analyzed by Sinclair & Zeppelin (2002) and Trites et al. (2007b) were collected from rookeries dominated by adult females. Thus, differences in summer diet composition and diversity between studies may be, in part, due to age- and sex-specific differences in foraging behavior. At other times of the year scats have been collected from haulouts, which typically have a more diverse age and sex structure and are generally thought to be representative of the popu-

lation as a whole. Future studies focused on age- and sex-specific diet may help in interpreting differences in regional and temporal diet composition, but, for many locations, segregated sites do not occur or are inaccessible. The use of DNA-based techniques for sex assignment of scats (e.g. Reed et al. 1997) may allow assessment of sources of variation in diet composition in future studies.

CONCLUSIONS

Our study presents the most comprehensive and recent description of the diet of Steller sea lions in the Kodiak Archipelago. The prey species identified in our study were relatively similar to the suite of prey consumed by sea lions in the 1990s, but differed markedly in their relative importance. Unlike diet studies in the 1990s, pollock was not the most dominant prey species. Although pollock was ranked second in importance overall based on frequency of occurrence, the contribution of pollock to the diet of Steller sea lions in the Kodiak Archipelago varied significantly among regions, seasons, and years. In contrast, sand lance was ranked the most dominant prey overall and was relatively consistent in importance across all regions, seasons, and years. In addition to sand lance, herring and capelin also appear to be important energy-rich prey for sea lions during part of the year. Unlike other dominant species that varied in their contribution from year to year, sand lance and herring were consistently dominant in the north in winter and in the west in spring, respectively. Thus, during the non-breeding season, sand lance and herring may provide a predictable and energy-rich prey resource for sea lions in the Kodiak Archipelago. The importance of these small forage species in the diet of sea lions may also be underestimated due to biases inherent in diet studies based on scat analysis.

As we predicted, the diet composition of Steller sea lions varied among geographical regions, most likely reflecting the influence of physical and oceanographic conditions on local prey availability. Pollock and Pacific cod were more important in the east compared to other regions, whereas arrowtooth flounder was more important in the north, herring in the west, and salmon in the south, at least over summer. Integration of concurrent fine-scale investigations into the local availability of prey will likely shed light on the diet variability and distribution of Steller sea lions. However, understanding how local- and broad-scale changes in prey availability and climatic conditions influence the population dynamics of sea lions will ultimately require a greater understanding of the spatial foraging behavior of Steller sea lions and how the temporal and spatial availability of prey affects diet choice of different age and sex groups.

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