

Abstract—The diet of Steller sea lions (*Eumetopias jubatus*) was determined from 1494 scats (feces) collected at breeding (rookeries) and nonbreeding (haulout) sites in Southeast Alaska from 1993 to 1999. The most common prey of 61 species identified were walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes hexapterus*), Pacific salmon (Salmonidae), arrowtooth flounder (*Atheresthes stomias*), rockfish (*Sebastes* spp.), skates (Rajidae), and cephalopods (squid and octopus). Steller sea lion diets at the three Southeast Alaska rookeries differed significantly from one another. The sea lions consumed the most diverse range of prey categories during summer, and the least diverse during fall. Diet was more diverse in Southeast Alaska during the 1990s than in any other region of Alaska (Gulf of Alaska and Aleutian Islands). Dietary differences between increasing and declining populations of Steller sea lions in Alaska correlate with rates of population change, and add credence to the view that diet may have played a role in the decline of sea lions in the Gulf of Alaska and Aleutian Islands.

Diets of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska, 1993–1999

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Steller sea lion (*Eumetopias jubatus*) populations in the Aleutian Islands and Gulf of Alaska began declining in the mid-1970s and were listed as endangered under the U.S. Endangered Species Act in 1997 (NMFS¹; Trites and Larkin, 1996; Loughlin, 1998). The cause of the population decline is uncertain but may be linked to a decrease in the quantity, quality, or availability of prey, in turn caused either by commercial fisheries or by a natural change in the ecosystem (Alaska Sea Grant, 1993; DeMaster and Atkinson, 2002; Trites et al., 2007). Stomach contents and scat analysis indicate that the diets of the declining population may have changed from primarily small, fatty, schooling fishes (such as capelin (*Malotus villosus*) and sand lance (*Ammodytes hexapterus*)) in the 1950s to one increasingly dominated by walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius*), and flatfish (Pleuronectidae) in the 1970s, 1980s, and 1990s (Mathisen et al., 1962; Thorsteinson and Lensink, 1962; Pitcher, 1981; Calkins and Goodwin¹; Merrick et al., 1997; Sinclair and Zeppelin, 2002).²

Merrick et al. (1997) found a positive relationship between the rate of population change and the diversity of summer Steller sea lion diets in the declining population during the early 1990s. Regions that had the highest

rates of decline had the lowest diversities of diet. The greater the diet diversity, the slower the rate of population decline. Additional diet data (through to 2001) supported the conclusion that diet diversity had some influence on population success (Sinclair and Zeppelin, 2002; Sinclair et al., 2005). Merrick et al. (1997) hypothesized that animals with less diverse diets may have experienced difficulty obtaining enough prey. Others have hypothesized that consumption of larger proportions of lower energy-dense prey may have exacerbated the effect of diet diversity by increasing the food requirements of sea lions (Alverson, 1992; Rosen and Trites, 2000; Trites and Donnelly, 2003). Sea lions with less diverse, low energy-dense diets may also have been more sensitive to changes in overall prey abundance, and could have theoretically incurred higher rates of predation from killer

¹ NMFS (National Marine Fisheries Service). 1992. Recovery plan for the Steller sea lion (*Eumetopias jubatus*), 92 p. Prepared by the Steller Sea Lion Recovery Team for the National Marine Fisheries Service, 1315 East-West Highway, Silver Spring, MD 20910-3282.

² Calkins, D. G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska, 76 p. Unpublished report. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518-1599.

whales if they had to forage for longer periods of time.

Population trends in Southeast Alaska have been opposite to those observed in the Gulf of Alaska (Trites and Larkin, 1996; Calkins et al., 1999; Pitcher et al., 2007). The robustness of the Southeast population compared to the other regions of Alaska may reflect a difference in diet. One explanation for this finding is that Steller sea lions in Southeast Alaska eat a wider range of prey and therefore have a more diverse diet. Another is that low energy-density prey (such as pollock) do not comprise a significant portion of the sea lion diet in Southeast Alaska.

Our goal was to determine the diets of Steller sea lions in Southeast Alaska. We sought to test two hypotheses: 1) diet in Southeast Alaska is the most diverse of all regions inhabited by Steller sea lions; and 2) pollock is not an important prey species in Southeast Alaska. We also wanted to document prey associations and seasonal changes in diet.

Materials and methods

There are three major breeding areas (rookeries) and over 45 major non-breeding areas (haulouts) in Southeast Alaska. We collected 1494 scats from 12 haulouts and all three rookeries from 1993 through 1999 (Fig. 1). Some areas, such as the Forrester rookery, were sampled every year, and others were sampled less frequently (Table 1). We grouped our analyses into rookeries and haulouts, and then into subgroups by sample size, location, and frequency of sampling. Haulouts consisted of 12 nonbreeding sites in the inside protected waters of Southeast Alaska (Fig. 1). Rookeries consisted of the three breeding areas in Southeast Alaska (Forrester Island, Hazy Island, and White Sisters Islands).

Scats were generally collected opportunistically, when rookeries and haulouts were disturbed in order to count pups or for other research purposes. Each scat was placed in a zip-lock plastic bag and frozen in a 5-gallon plastic bucket before it was shipped to the Food and Energy Consumption Laboratory at the Vancouver Aquarium Marine Science Centre for cleaning. Only scats that were big enough or solid enough to likely contain prey remains were collected, and only one scat was collected from any group of scats if there was any doubt about whether the scat came from more than one Steller sea lion. Each thawed scat was transferred to a plastic jar and soaked in water for 1–6 days. Periodic

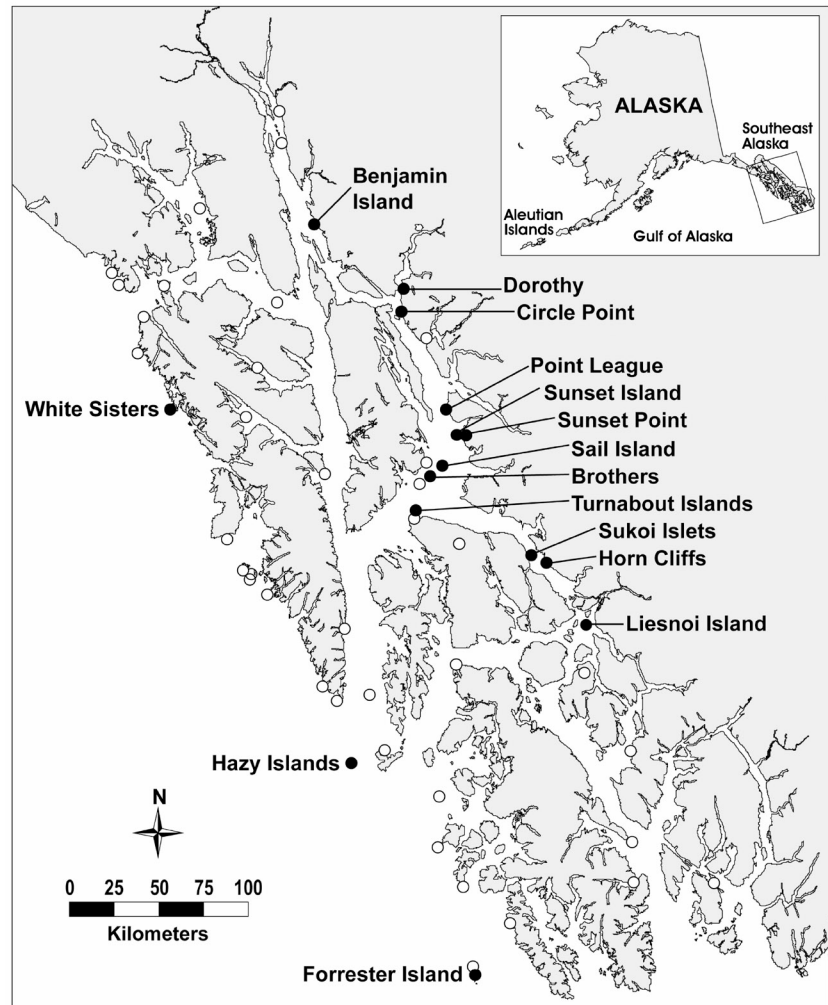


Figure 1

Major rookeries (White Sisters, Hazy Island, and Forrester Island) and haulouts (all other sites) of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska during 1993–99. Labeled sites indicate where scats were collected.

shaking of the jars ensured that the scats broke down and formed a uniform slurry at the bottom of the jar. Volume was recorded from graduated markings on each jar. An elutriator removed most of the water-soluble elements (Bigg and Olesiuk, 1990) before the remaining sample was washed through a fine mesh screen.

Prey species were identified at Pacific IDentifications Inc. (Victoria, BC) from cleaned and dried hard parts; the types of hard parts that were present and the species from which they came were also noted. Prey hard parts recovered from scats were compared with hard parts from a reference collection of identified skeletal and nonskeletal hard parts. Otoliths and all other hard parts were identified to the lowest possible taxon. Hard parts that were digested beyond recognition or were not diagnostic for prey taxa were not included in our analysis (e.g., ribs). Some recovered structures, such as otoliths or squid beaks, could be used to estimate

the type and number of prey consumed, but other hard parts, such as scales, teeth, branchials, and gill rakers, could only be used to quantify the type of prey consumed.

Scats that were empty or contained prey that could not be identified with certainty were not analyzed. These represented few of the scats collected (56 of 1494, 4%). Unrecognizable hard parts could have been from

Table 1

Total number of Steller sea lion (*Eumetopias jubatus*) scats collected in Southeast Alaska during 1993–99 by year, location, and month. Note that North Rocks, Cape Horn Rocks, and Sea Lion Rocks are part of the Forrester Island rookery complex.

Year	Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1993	Benjamin Is.	0	0	0	0	0	0	0	0	0	0	28	0	28
1993	Brothers	0	0	0	0	0	0	0	0	0	7	27	0	34
1993	Cape Horn Rocks	0	0	0	0	0	5	0	0	0	0	0	0	5
1993	Hazy	0	0	0	0	0	27	0	0	0	0	0	0	27
1993	North Rocks	0	0	0	0	0	8	0	0	0	0	0	0	8
1993	Pt. League	0	0	0	0	0	0	0	0	0	0	38	0	38
1993	Sail Is.	0	0	0	0	0	0	0	0	0	0	80	0	80
1993	Sea Lion Rocks	0	0	0	0	0	9	8	0	0	0	0	0	17
	Total	0	0	0	0	0	49	8	0	0	7	173	0	237
1994	Cape Horn Rocks	0	0	0	0	0	29	0	0	0	0	0	0	29
1994	Hazy	0	0	0	0	0	0	54	0	0	0	0	0	54
1994	North Rocks	0	0	0	0	0	32	0	0	0	0	0	0	32
1994	Sea Lion Rocks	0	0	0	0	0	73	0	0	0	0	0	0	73
1994	White Sisters	0	0	0	0	0	0	49	0	0	0	0	0	49
	Total	0	0	0	0	0	134	103	0	0	0	0	0	237
1995	Benjamin Is.	0	0	0	0	0	0	0	0	0	16	0	0	16
1995	Brothers	0	0	0	0	0	0	0	0	0	25	0	14	39
1995	Cape Horn Rocks	0	0	0	0	0	30	0	0	0	0	0	0	30
1995	Circle Pt.	0	0	0	0	0	0	0	0	0	12	0	22	34
1995	Horn Cliff	0	0	0	0	0	0	0	0	0	10	0	0	10
1995	North Rocks	0	0	0	0	0	68	0	0	0	0	0	0	68
1995	Pt. League	0	0	0	0	0	0	0	0	0	13	0	14	27
1995	Sail Is.	0	0	0	0	0	0	0	0	0	26	0	6	32
1995	Sea Lion Rocks	0	0	0	0	0	30	0	0	0	0	0	0	30
1995	Sukoi Is.	0	0	0	0	0	0	0	0	0	7	0	0	7
1995	Sunset Is.	0	0	0	0	0	0	0	0	0	0	0	4	4
1995	Sunset Pt.	0	0	0	0	0	0	0	0	0	0	0	22	22
1995	Turnabout Is.	0	0	0	0	0	0	0	0	0	10	0	2	12
	Total	0	0	0	0	0	128	0	0	0	119	0	84	331
1996	Benjamin Is.	4	0	10	0	0	0	0	0	0	0	0	0	14
1996	Brothers	0	0	15	20	18	0	0	0	0	0	0	0	53
1996	Cape Horn Rocks	0	0	0	0	0	11	13	0	0	0	0	0	24
1996	Dorothy	0	0	0	11	0	0	0	0	0	0	0	0	11
1996	Horn Cliff	0	0	0	0	12	0	0	0	0	0	0	0	12
1996	Liesnoi Is.	0	0	0	0	22	0	0	0	0	0	0	0	22
1996	North Rocks	0	0	0	0	0	0	21	0	0	0	0	0	21
1996	Pt. League	0	0	11	0	14	0	0	0	0	0	0	0	25
1996	Sail Is.	0	0	0	0	11	0	0	0	0	0	0	0	11
1996	Sea Lion Rocks	0	0	0	0	0	8	0	0	0	0	0	0	8
1996	Sunset Pt.	0	0	20	13	0	0	0	0	0	0	45	0	78
1996	Turnabout Is.	0	0	34	0	0	0	0	0	0	0	0	0	34
	Total	4	0	90	44	77	19	34	0	0	0	45	0	313

continued

species not in the reference skeleton collection at the time of identification or could have been too far digested to be identifiable.

We grouped the identified species of prey into eight categories for statistical analysis. These included gadids, forage fish, salmon (*Salmonidae*), flatfish, rockfish (*Sebastes* spp.), cephalopods, hexagrammids, and other prey (Fig. 2). Scats that contained more than one species from a particular group were scored as containing only a single occurrence of that group. For example, a scat containing both Pacific herring (*Clupea pallasii*) and sand lance was scored as having a single occurrence of forage fish. Hexagrammids do not inhabit the waters of Southeast Alaska in significant numbers but were included as a prey category so that diets could be compared across regions of the North Pacific where hexagrammids are consumed in greater numbers (Merrick et al., 1997; Sinclair and Zeppelin, 2002).

The diversity of the diet was calculated for the eight prey groups by using the Shannon-Wiener species diversity index (Ricklefs and Miller, 2000), which yields a value between 1 and 8, where a value of 1 indicates that only one of the eight groups was consumed, and a value of 8 indicates that all eight were equally consumed. Merrick et al. (1997) used this index to determine the dietary diversity of Steller sea lions that consumed seven prey groups in the Gulf of Alaska and Aleutian Islands. We therefore pooled rockfish with other prey to create the same seven categories used by Merrick et al. (1997) to compare the diversity of diet across all regions of Alaska. We compared our estimate of dietary diversity to those presented by Merrick et al. (1997) for diet data collected between 1990 and 1995. However, we recalculated the diet diversities presented in their paper (from their split-sample frequency of oc-

currence data) because of a calculation error in their published values.

Seasonal diets were calculated for rookeries in summer (Forrester Island, Jun–Aug, 1993–99) and haulouts in fall (Sep–Nov, 1993 and 1995–96), winter (Dec–Feb, 1996–1997), and spring (Mar–May 1996). Average summer diet (Jun–Aug) was calculated from the three rookeries—weighted by the average number of pups counted at each site during 1993–1997 (pup counts serving as an index of population size; Trites and Larkin, 1996; Pitcher et al., 2007). The summer data were weighted to indicate what the average Steller sea lion ate in Southeast Alaska, rather than to describe what the average rookery diet was. Fall, winter, and spring diets were given equal weight and averaged to describe the nonsummer diet (haulouts, Sep–May) because animals are more evenly distributed during the nonbreeding season and haulout counts were not available for each of the seasons.

The relative importance of prey in the diet was quantified as “simple” and “split-sample” frequency of occurrences. The simple frequency of occurrence indicates what proportion of scats contains any particular prey type. They do not sum to 100%. For example, 80% of the scats examined may contain gadids, and 50% may contain forage fish—meaning that some scats contained both prey types, and others contained only gadids or only forage fish. The second method we used, the split-sample frequency of occurrence (Olesiuk et al., 1990; Olesiuk, 1993), yields the proportion of the overall diet made up of any single prey type. These proportions do sum to 100%. With the split-sample method, it is assumed that the scat contained remains from all prey consumed in the previous meal and that the prey were consumed in equal volumes.

Table 1 (continued)

Year	Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1997	Cape Horn Rocks	0	0	0	0	0	25	0	0	0	0	0	0	25
1997	North Rocks	0	0	0	0	0	25	0	0	0	0	0	0	25
1997	Sea Lion Rocks	0	0	0	0	0	25	0	0	0	0	0	0	25
1997	Sunset Pt.	0	32	0	0	0	0	0	0	0	0	0	0	32
1997	Turnabout Is.	0	27	0	0	0	0	0	0	0	0	0	0	27
	Total	0	59	0	0	0	75	0	0	0	0	0	0	134
1998	Cape Horn Rocks	0	0	0	0	0	0	27	0	0	0	0	0	27
1998	Hazy	0	0	0	0	0	0	70	0	0	0	0	0	70
1998	North Rocks	0	0	0	0	0	0	21	0	0	0	0	0	21
1998	Sea Lion Rocks	0	0	0	0	0	0	21	0	0	0	0	0	21
	Total	0	0	0	0	0	0	139	0	0	0	0	0	139
1999	Hazy	0	0	0	0	0	0	60	0	0	0	0	0	60
1999	North Rocks	0	0	0	0	0	6	33	0	0	0	0	0	39
1999	Sea Lion Rocks	0	0	0	0	0	4	0	0	0	0	0	0	4
	Total	0	0	0	0	0	10	93	0	0	0	0	0	103
Grand Total		4	59	90	44	77	415	377	0	0	126	218	84	1494

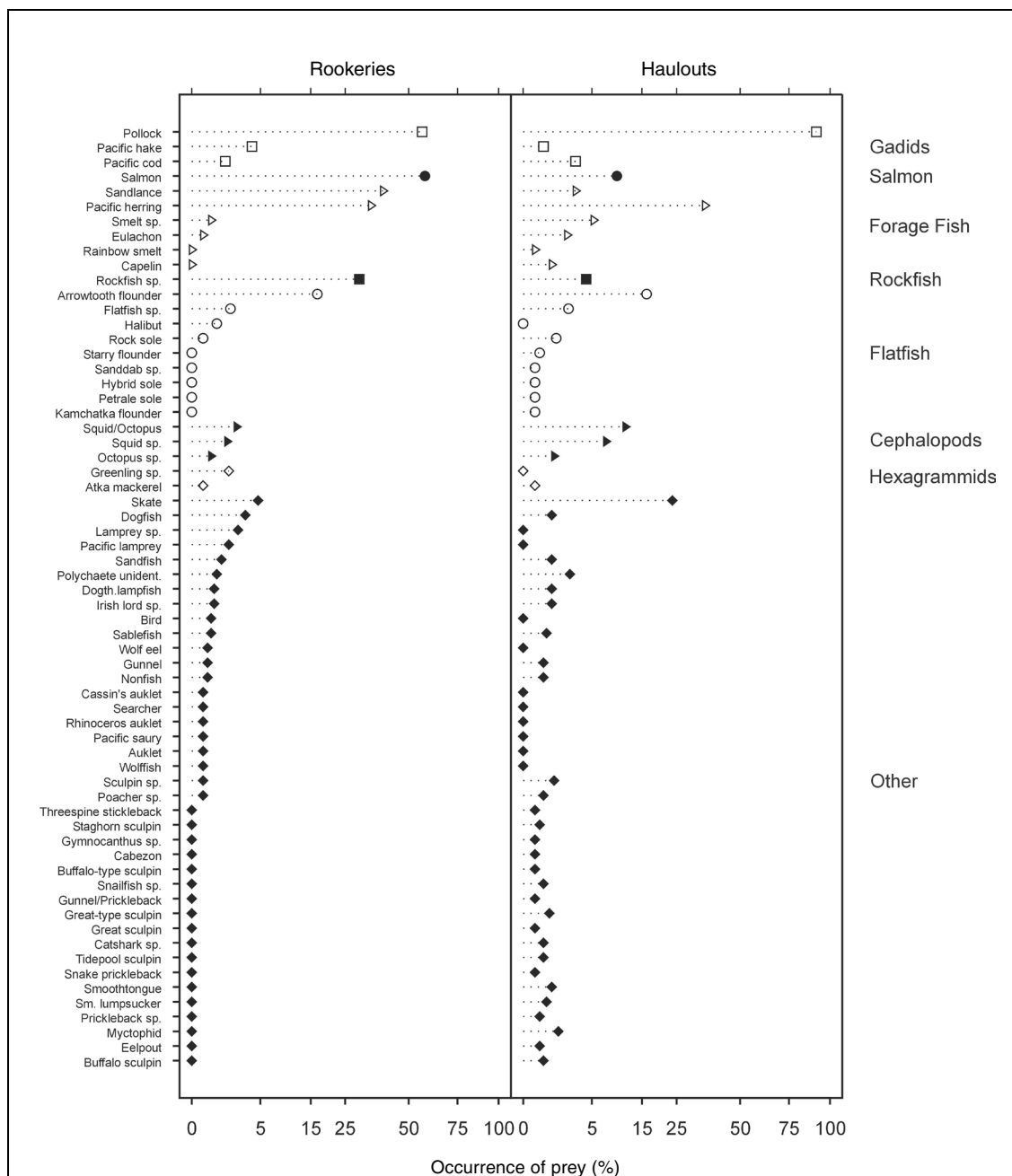


Figure 2

Frequency of occurrence of individual prey species in Steller sea lion (*Eumetopias jubatus*) scats from three Southeast Alaskan rookeries (Forrester, Hazy, and White Sisters; $n=752$) in summer (Jun–Aug) and haulouts ($n=686$) during the rest of the year (Sep–May, 1993–99). Data were pooled across months, years, and sites. Plotted data were transformed (square-root transformed) to improve the visual resolution at lower frequencies of occurrence. The eight symbols identify the eight groups of species used to calculate diet diversity.

Statistical analyses were performed on the simple frequency of occurrences to determine whether diets varied by sites and time (across years). We used a contingency table analysis for the total number of scats containing particular prey categories

(Pearson χ^2 , $\alpha \leq 0.05$). The cephalopod and hexagrammid prey categories were not considered in these analyses because of their low frequencies of occurrence. Differences in the number of categories of prey consumed on each foraging trip (i.e., the number of prey

groups per scat) were compared by using analysis of variance.

Associations between prey groups recovered from individual scats were identified by calculating partial correlation coefficients for each pair of prey groups by using presence and absence data with each scat as a replicate (Zar, 1996). This analysis was performed for all scats collected at the three rookeries during the summer and for all scats collected at the haulouts during autumn–spring. Partial correlations were considered significant at $P=0.05$. Prey associations were illustrated by using the *hclust* function of S-Plus 2000 (Mathsoft Inc., Seattle, WA) and using the “average” clustering method and the distance between two prey groups as equal to 1 minus the partial correlation coefficient of those two prey.

Results

A total of 61 species of prey were identified from all of the scats examined. The most common prey (i.e., those that occurred in more than 5% of all the scats examined) in order of frequency were walleye pollock, Pacific herring, sand lance, salmon, arrowtooth flounder (*Atheresthes stomias*), rockfish (*Sebastes* spp.), skates (Rajidae), squid, and octopus (Fig. 2, Table 2). Species of salmon, rockfish, squids, and octopus could be identified only to family, and other species, such as Pacific herring or walleye pollock, could be identified to species. Unfortunately not all recovered hard parts could be identified to the species level.

Steller sea lion diets at the Forrester Island rookeries were significantly different from one another in 1994 and 1998 ($P<0.001$), but the differences between the diets at Forrester Island and those at Hazy Island in 1993 and 1999 were not significant ($P=0.06$, 0.36 , respectively; Fig. 3). At White Sisters, mature females consumed primarily forage fish followed by gadids; whereas at Hazy Island, gadids were the dominant prey. Further south at Forrester Island, the diet was more evenly distributed between forage fish, salmon, and gadids. Scats were collected in multiple years at Forrester Island and Hazy Island and showed little difference in diet over time within each site ($P=0.30$, 0.11 , respectively).

Outside of the breeding season, the diet of Steller sea lions in Southeast Alaska was dominated by gadids (primarily pollock; Figs. 4 and 5, Table 3). The abundance of salmon in the diet dropped from summer to fall (Fig. 4, Table 3) when the runs of salmon presumably passed into the river systems. Forage fish were found in 37% of the scats collected in the fall (Sep–Nov), in 43% of scats in the winter, 47% in spring, and in 62% of scats in the summer (Fig. 4). Squid and octopus were more important in fall and winter (22% on average) than during summer. Rockfish were consumed relatively frequently during the summer but were largely absent in the diet from fall to spring, presumably because they were not present or accessible in significant numbers. “Other” fishes (primarily

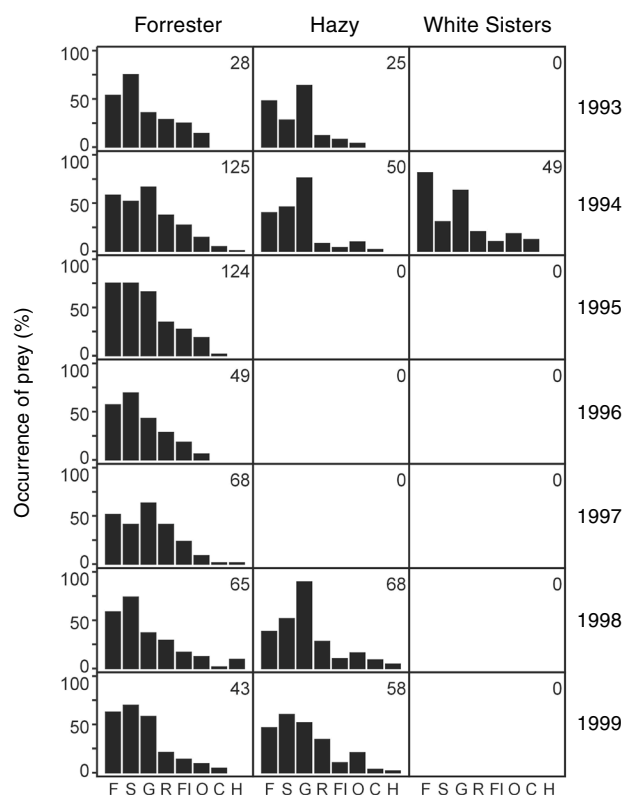


Figure 3

Frequency of occurrence of prey types in Steller sea lion (*Eumetopias jubatus*) scats by year from three Southeast Alaskan rookeries (Forrester, Hazy, and White Sisters) in summer (Jun–Aug). Types of prey consumed were F = forage fish, S = salmon, G = gadids, R = rockfish, Fl = flatfish, O = other, C = cephalopods, and H = hexagrammids. Data were pooled across months. Sample sizes shown in each panel indicate number of scats.

skates, see Fig. 2) rose in importance from summer to fall (13% to 24% respectively), peaking at 50% in winter (Fig. 4). Gadids, forage fishes, and other fishes were the dominant prey during winter. In terms of diet diversity (dd), Steller sea lions consumed the most diverse range of prey categories during summer at rookeries (dd=5.34 on a scale of 1–8), and the least diverse during fall while at haulouts (dd=3.53).

Most scats contained at least two prey groups, and one scat contained remains from all eight groups (Fig. 6). The mean number of prey groups per scat ranged from 2.1 to 2.6 depending on season (Fig. 6). In general, the distributions were skewed towards fewer prey groups occurring together in a single scat in fall and spring, and were more normally distributed in summer and winter. The number of prey types per scat was not significantly different between fall and spring or between summer and winter ($P>0.05$; Tukey-Kramer test) but did differ significantly between these seasonal pairings. Those scats with only a single identifiable prey type

Table 2

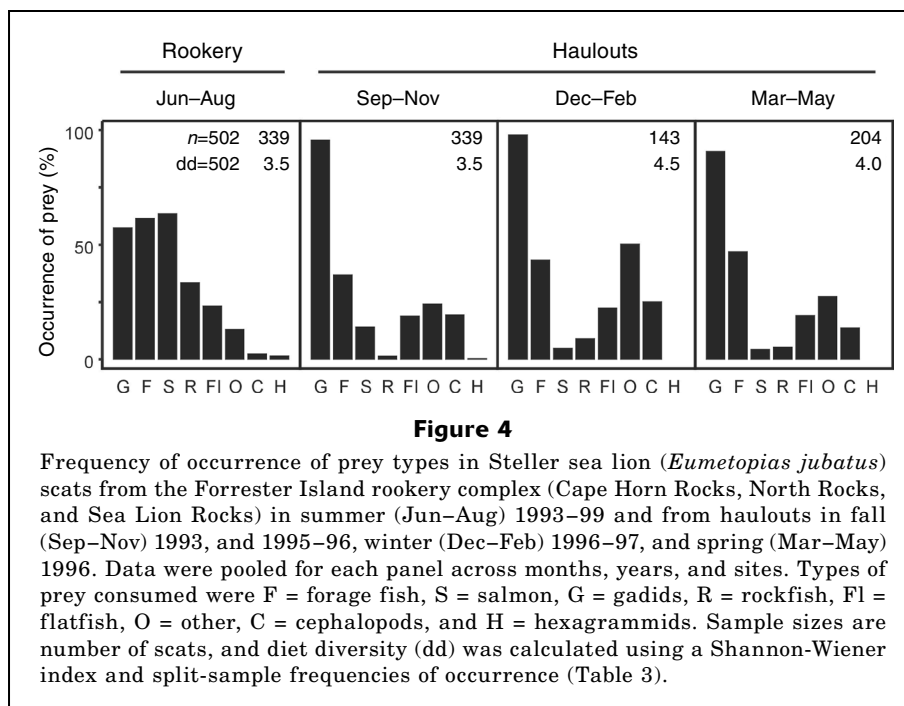
Frequency of occurrence of prey types in Steller sea lion (*Eumetopias jubatus*) scats from Southeast Alaska. Samples were from rookeries (Forrester, Hazy, and White Sisters) in summer (Jun–Aug) 1993–99 and from haulouts in fall (Sep–Nov) 1993 and 1995–96, winter (Dec–Feb) 1996–97, and spring (Mar–May) 1996. The rookery data (summer) were pooled across months (and sites within the Forrester complex) but averaged across years and rookeries (weighted by pup counts). Haulout data were pooled across months and sites but averaged across years.

Species	Frequency of occurrence in diet (%)				Species	Frequency of occurrence in diet (%)			
	Summer <i>n</i> =752	Fall <i>n</i> =339	Winter <i>n</i> =143	Spring <i>n</i> =204		Summer <i>n</i> =752	Fall <i>n</i> =339	Winter <i>n</i> =143	Spring <i>n</i> =204
Gadids					Other species				
Walleye pollock	56.4	90.6	96.5	88.7	Skate	4.7	17.7	45.5	18.1
Pacific hake	3.9	0.9	0.0	0.0	Dogfish	3.1	1.5	0.0	0.5
Pacific cod	1.2	2.4	2.1	4.4	Lamprey spp.	2.3	0.0	0.0	0.0
Salmonids					Pacific lamprey	1.5	0.0	0.0	0.0
Salmon	57.7	14.2	4.9	4.4	Sandfish	0.9	0.6	0.0	2.0
Forage fish					Polychaete unident.	0.7	0.6	6.3	2.5
Pacific sand lance	38.8	3.8	2.8	1.5	Dogfish lampfish	0.5	0.0	0.7	2.5
Pacific herring	34.0	31.3	39.9	38.2	Irish lord spp.	0.5	0.6	1.4	1.0
Smelt spp.	0.4	5.0	2.8	7.4	Sablefish	0.4	1.2	0.0	0.0
Eulachon	0.1	0.0	2.1	5.4	Wolf eel	0.3	0.0	0.0	0.0
Rainbow smelt	0.0	0.3	0.0	0.0	Gunnel	0.3	0.3	0.7	0.5
Capelin	0.0	0.6	0.0	2.0	Searcher	0.1	0.0	0.0	0.0
Rockfish					Pacific saury	0.1	0.0	0.0	0.0
Rockfish spp.	29.8	1.5	9.1	5.4	Wolffish	0.1	0.0	0.0	0.0
Flatfish					Sculpin spp.	0.1	1.5	1.4	0.0
Arrowtooth flounder	16.8	16.2	20.3	13.2	Poacher spp.	0.1	0.9	0.0	0.0
Flatfish spp.	1.6	1.8	2.1	2.9	Threespine stickleback	0.0	0.0	0.0	0.5
Halibut	0.7	0.0	0.0	0.0	Staghorn sculpin	0.0	0.0	0.0	1.0
Rock sole	0.1	0.9	0.7	2.0	Gymocanthus spp.	0.0	0.0	0.0	0.5
Starry flounder	0.0	0.0	0.0	1.0	Cabezon	0.0	0.0	0.0	0.5
Sanddab spp.	0.0	0.0	0.0	0.5	Buffalo-type sculpin	0.0	0.0	0.0	0.5
Hybrid sole	0.0	0.0	0.0	0.5	Snailfish spp.	0.0	0.0	0.7	1.0
Petrale sole	0.0	0.3	0.0	0.0	Gunnel/Prickleback	0.0	0.0	0.7	0.0
Kamchatka flounder	0.0	0.3	0.0	0.0	Great-type sculpin	0.0	0.0	1.4	1.5
Cephalopods					Great sculpin	0.0	0.0	0.7	0.0
Squid/Octopus	2.1	11.2	20.3	4.4	Catshark spp.	0.0	0.0	1.4	0.5
Squid spp.	1.3	8.0	4.9	7.8	Tidepool sculpin	0.0	0.3	0.7	0.5
Octopus spp.	0.4	1.2	0.0	1.5	Snake prickleback	0.0	0.3	0.0	0.0
Hexagrammids					Smoothtongue	0.0	0.3	2.8	0.5
Greenling spp.	1.5	0.0	0.0	0.0	Small lumpsucker	0.0	0.6	0.7	0.5
Atka mackerel	0.1	0.3	0.0	0.0	Prickleback spp.	0.0	0.3	0.0	0.5
					Myctophid	0.0	1.2	3.5	0.0
					Eelpout	0.0	0.3	0.0	0.5
					Buffalo sculpin	0.0	0.9	0.0	0.0

more likely contained gadids (mostly pollock) than any other species.

There was a positive relationship between scat size (volume) and the numbers of prey types each scat contained for samples <250 mL (which represented about 50% of the scats collected). Beyond this volume, numbers of prey types per scat appeared to be independent of scat size (Fig. 7).

In terms of which prey groups occurred most frequently together, the highest partial correlation among prey groups was between salmon and forage fish (rookeries: $r=0.23$, $r_{0.05(2),744}=0.07$, $P<0.05$; haulouts: $r=0.189$, $r_{0.05(2),678}=0.08$, $P<0.05$; Fig. 8). Gadids and cephalopods were also significantly correlated in scats from both rookeries ($r=0.11$) and haulouts ($r=0.08$), whereas gadids were negatively correlated with occurrences of salmon

**Table 3**

Split-sample frequency of occurrence of prey types in Steller sea lion (*Eumetopias jubatus*) scats from Southeast Alaska. Samples were from rookeries (Forrester, Hazy, and White Sisters) in summer (Jun–Aug) 1993–99 and from haulouts in fall (Sep–Nov) 1993 and 1995–96, winter (Dec–Feb) 1996–1997, and spring (Mar–May) 1996. The rookery data (summer) were pooled across months (and sites within the Forrester complex) but averaged across years and rookeries (weighted by pup counts). Haulout data were pooled across months and sites, but were averaged across years.

Season	Prey category (%)							
	Cephalopods	Flatfish	Forage fish	Gadids	Hexagrammids	Other	Rockfish	Salmon
Winter (Dec–Feb)	8.1	7.6	13.5	49.1	0.0	15.9	4.5	1.2
Spring (Mar–May)	5.0	7.6	21.0	52.5	0.0	10.5	2.0	1.4
Summer (Jun–Aug)	0.8	6.4	21.9	27.3	0.4	4.3	11.7	27.3
Fall (Sep–Nov)	7.0	6.2	12.5	62.2	0.1	8.4	0.4	3.3

from rookeries ($r = -0.16$) and with forage fish from scats collected at haulouts ($r = -0.10$).

Plotting our estimate of dietary diversity for Southeast Alaska during summer with values recalculated for other regions of Alaska revealed a significant relationship between diet diversity and the rate of population change during 1990–94 (Fig. 9). High rates of population decline correlated with low levels of diet diversity.

Discussion

The Southeast Alaska population of Steller sea lions grew considerably since the first census of 100 animals was made at Forrester Island in the 1920s (Rowley,

1929). Subsequent counts were 350 sea lions (nonpups) in 1945 (Imler and Sarber, 1947), and 2500 in 1957 (Mathisen and Lopp, 1963). The total population in 1992 (including pups) was estimated at 10,003 (Trites and Larkin, 1996), and an annual growth rate of 6% was estimated (1979–97; Calkins et al., 1999). Steller sea lions were first noted breeding on White Sisters (3 pups) and Hazy Island (30 pups born) in 1979. In 1997, 205 pups were counted at White Sisters, 1157 were counted at Hazy, and 2798 were counted at Forrester Island. Small numbers of pups have since been noted at Graves Rocks and Biali Rocks (Pitcher et al., 2007).

It is not clear why Steller sea lion populations grew through the 20th century in Southeast Alaska. One possible explanation is that predation by killer whales

or hunting by native peoples was reduced. Another is that these sea lions may have begun consuming more abundant prey or they had a higher quality diet that enhanced birth and survival rates. Unfortunately there is little or no information to shed light on this important question.

There are few data available on fish stocks preyed upon by sea lions or on the diet of Steller sea lions in Southeast Alaska prior to the 1990s. Pollock does not appear to have been abundant in fishery surveys and was not thought to be present in commercially available quantities. However, Imler and Sarber (1947) reported that pollock were found in five of the seven stomachs taken in the vicinity of the Brothers Islands and White Sisters Islands in 1946—and accounted for 68% of the stomach contents by volume. The only other dietary information comes from the stomachs of five Steller sea lions shot at Forrester Island in May 1986 (Calkins and Goodwin¹); for these sea lions Pacific cod (*Gadus macrocephalus*) accounted for the largest single

prey occurrence at 58% of the total volume, and pollock accounted for 32% of the contents by volume and were present in three stomachs.

The scats we collected during the 1990s revealed that gadids were an important part of the diet and that pollock was the predominant gadid. Relatively few Pacific cod were noted (Fig. 2). Pollock were the most frequently occurring food item in all scats examined from haulouts during the nonbreeding season and were second only to salmon by frequency of occurrence in all scats taken from rookeries during the breeding season. Pollock may have been important in the diet of Steller sea lions in the 1940s and 1980s, but the sample sizes taken at that time are inadequate to draw a firm conclusion or to determine whether diet changed over time (Trites and Joy, 2005).

Attempts to reconstruct the size of the pollock consumed during the 1990s in Southeast Alaska from the lengths of bones recovered in the scats revealed that adult fish (>45 cm fork length) were present more frequently in the diets of Steller sea lions on the outer coast sites than they were present in the diets of Steller sea lions from the inside waters (Tollit et al., 2004a). The largest proportions of fish consumed were of adult and subadult sizes. Juvenile pollock (≤ 20 cm) contributed insignificantly to the overall sea lion diet (Tollit et al., 2004a).

Potential biases

The use of scats, like all measures to quantify diet, entails caveats. Fortunately, the assumptions that underlie our analyses in Southeast Alaska also underlie the interpretation of scats we sought to compare them with from the Gulf of Alaska and Aleutian Islands. Some of the limitations that can restrict the interpretation of the dietary data from scats collected during the 1990s from all parts of Alaska are also greatly reduced by the large sample sizes (>1000 scats) collected in both regions (Trites and Joy, 2005). However, greater caution must be exerted when comparing stomach contents of Steller sea lions shot from the 1950s–1980s with scats collected during the 1990s, particularly for species such as squid and octopus whose beaks can be caught on the stomach lining and are often regurgitated rather than passed through the intestinal tract.

Our seasonal diet estimates largely compared what lactating females were eating during summer with what lactating females and all other age and sex classes were eating during fall, winter, and spring. Whether or not the different age groups forage in different areas or have different prey preferences is not known. It should also be noted that the seasonal descriptions of diet came from samples that were primarily collected in two time periods—February to July (1996–99) and June to December (1993–95). Our conclusions about seasonal changes in diet could therefore be biased if significant changes occurred in the prey field over our decade of sampling. We assumed that feeding conditions remained relatively stable during the 1990s; our conclusions were based on

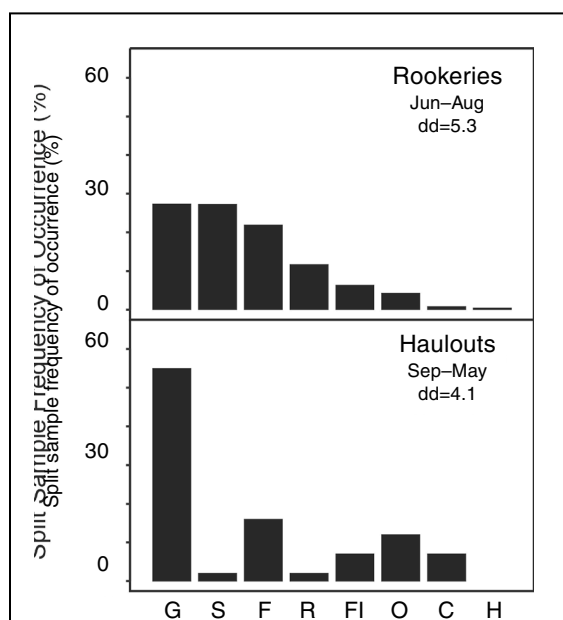
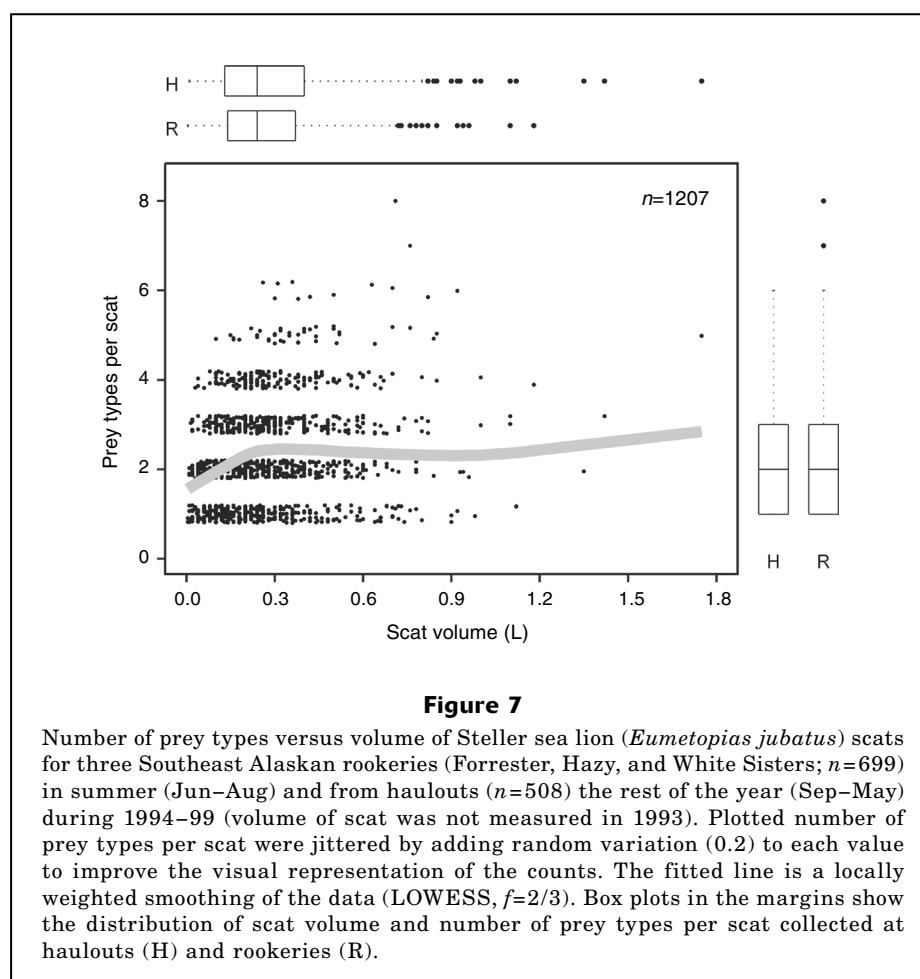
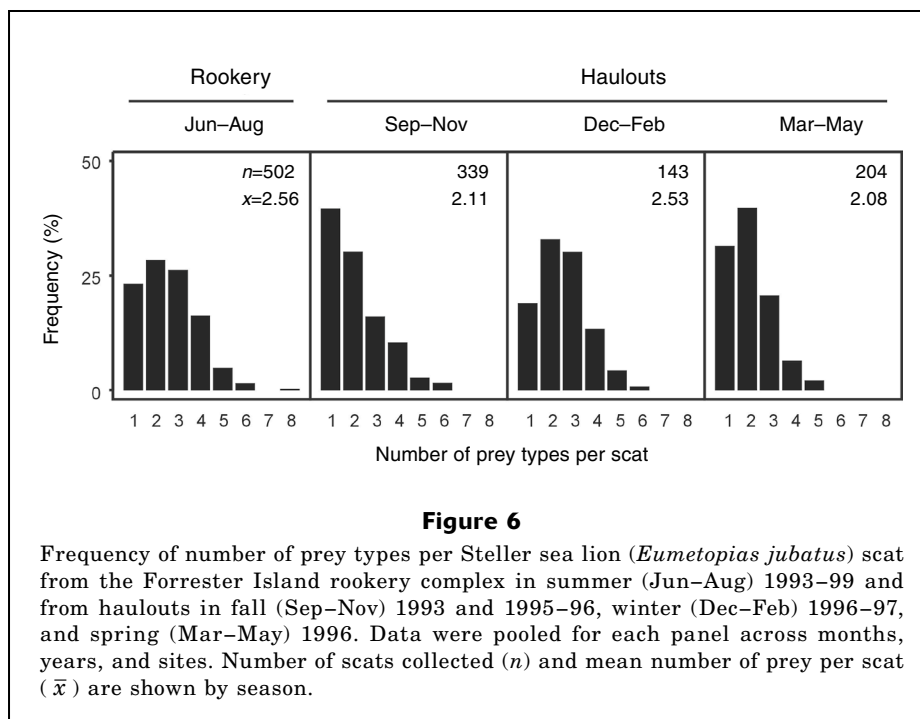
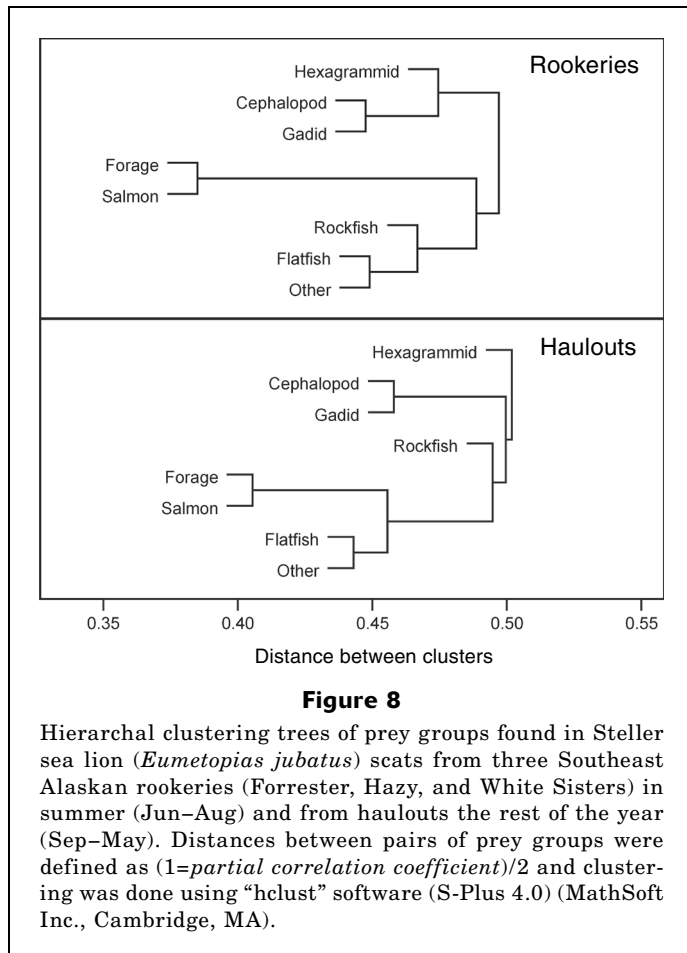


Figure 5

Split-sample frequency of occurrence of prey types in Steller sea lion (*Eumetopias jubatus*) scats from Southeast Alaskan rookeries (Forrester, Hazy, and White Sisters) in summer (Jun–Aug) and from haulouts the rest of the year (Table 1). Diet at rookeries is the weighted average (by the average 1993–97 pup counts) of the three mean rookery diets (averaged across years). The haulout diet is the average of the three mean seasonal diets (averaged across years). Diet diversity (dd) was calculated by using a Shannon-Wiener index. Types of prey consumed were F = forage fish, S = salmon, G = gadids, R = rockfish, FI = flatfish, O = other, C = cephalopods, and H = hexagrammids.

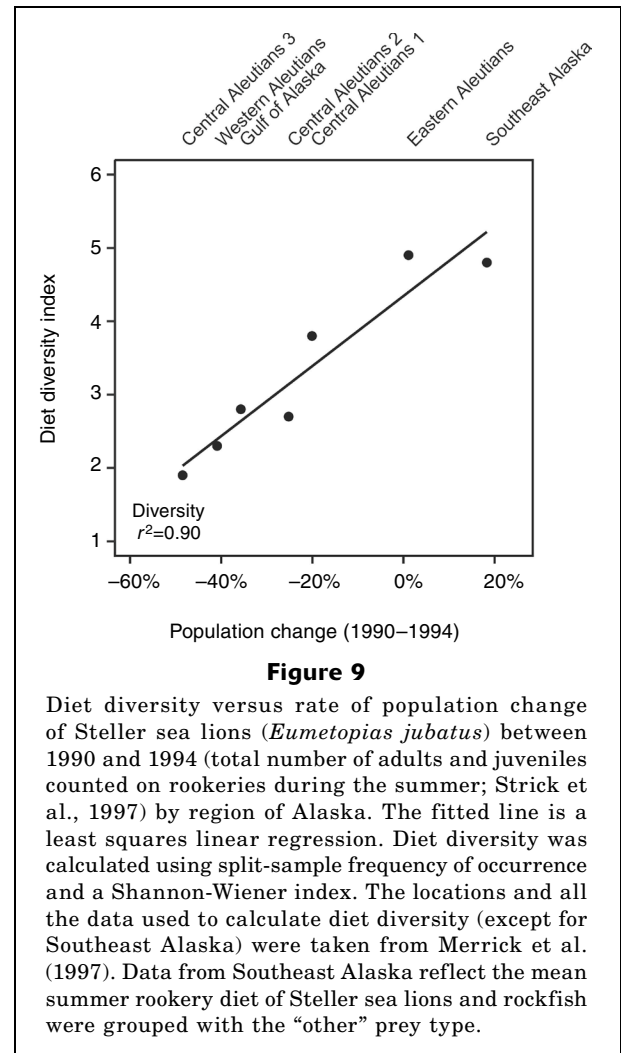




the consistency of the annual summer diet at Forrester Island (which was sampled in all years, Fig. 2) and on the relative stability of ocean conditions during the 1990s (which is believed to determine the relative abundances of suites of prey available to sea lions and other species; Benson and Trites, 2002; King, 2005; Trites et al., 2007). Thus we feel that the seasonal description of diet accurately reflects what Steller sea lions were eating in Southeast Alaska during the 1990s.

A bias could have been introduced in our analysis if the sizes of collected scats differed significantly between haulouts and rookeries, and if the number of prey species recovered was correlated with the size of scats. In checking this potential source of error, we found numbers of prey types per scat were positively related to size for scats <250 mL but were independent of scat size beyond this volume (Fig. 7). In general, there was little difference in the sizes of scats and numbers of species recovered from rookeries and haulouts, and thus there was no apparent effect of size of scat on our results.

By inferring the dietary importance of prey species from their frequencies of occurrence in scats one implicitly assumes that the probability of finding prey in scats is proportional to the number or mass of that prey consumed, and that this proportionality does not vary



among prey species. However, controlled feeding studies with captive Steller sea lions, and other pinnipeds, have shown that the types and proportions of prey hard parts that pass through the digestive tract vary, depending on the species of prey and the size of prey (Cottrell and Trites, 2002; Tollit et al., 2003; Tollit et al., 2004b). Pollock bones, for example, tend to be more robust than the bones of other species and have a higher likelihood of being recovered than the more fragile bones of other species, such as sand lance. However, smaller schooling species, such as sand lance, are likely to be consumed in higher numbers than pollock, and the greater consumption of these smaller species would increase the likelihood of some of the smaller bones passing through the digestive tract. Thus, the probability of detecting different prey species in scats can vary. Recording the presence of all identifiable hard parts as we did (i.e., not relying only on otoliths) significantly reduces the likelihood of any species passing undetected (Cottrell and Trites, 2002).

Captive feeding experiments indicate that the average scat probably contains the remains of prey con-

sumed over a number of days (Tollit et al., 2003). In other words, a scat likely does not represent a single meal, but is probably a composite of one or more feeding trips. Frequency of occurrence (Figs. 2–4) represents the probability that a particular prey type was consumed and does not represent the number or mass of prey consumed. However, with large sample sizes, the ranked importance of any particular prey type appears to equate with frequency of occurrence or numbers of prey (Sinclair et al., 1994; Antonelis et al., 1997; Sinclair and Zeppelin, 2002). The split-sample frequency of occurrence technique is another approach that deals with these biases by assuming that all prey species identified in a scat were consumed in equal mass and that each scat contributes an equal amount of information to the overall diet (Fig. 5, Table 3). Split-sample estimates tend to correlate with simple frequencies of occurrence to give a reasonable proportional description of diet, even when the assumption that all prey in a meal were consumed in equal quantities is not always true.

Prey associations

The remains found in sea lion scats likely delineate associations and distributions of prey species by region. In Southeast Alaska, the hard parts recovered from scats indicate that Steller sea lion prey were not randomly distributed, given that some prey species were found together more frequently than expected (if estimated occurrence was based on chance alone). For example, occurrences of gadids tended to be associated with occurrences of cephalopods (Fig. 8), whereas salmon were found most often with forage fishes (herring and sand lance). An association was also noted between flatfish and “other” species (primarily skates—Figs. 2 and 8). These associations may reflect groups of prey that are commonly associated with each other because of habitat similarities (e.g., depth or substrate similarities).

Associations of prey in scats may also reflect prey-specific foraging strategies of individual Steller sea lions. In some cases, prey associations may reflect secondary prey, whereby a species was consumed by the prey species actually targeted by the sea lion. Hard remains of a fish may occur in a sea lion scat not because it was depredated directly but because it had been consumed by a fish that was then eaten by a sea lion. In our case, 10 of over 60 species were found in more than 5% of the scats and were presumably preferred prey that were directly targeted by the sea lions (Fig. 2). The low frequencies of the remaining 50+ species (Fig. 2) may reflect preferred species that were in low abundance in Southeast Alaska, or they might indicate incidental prey and those that had been consumed by their preferred prey.

Eastern versus western diets

Our systematic survey of Steller sea lion diets in Southeast Alaska during the 1990s was prompted by a desire to gain insight into a possible dietary basis for the

population decline that occurred in the Gulf of Alaska and Aleutian Islands. Dietary differences of Steller sea lions between the two regions may help to explain why one population declined while the other increased.

The most common prey of 61 species identified in Southeast Alaska in frequency of occurrence were walleye pollock, Pacific herring, sand lance, salmon, arrowtooth flounder, rockfish, skates, squid, and octopus. Looking further afield (west) we found that Steller sea lions targeted a similar suite of species in the Gulf of Alaska in the 1990s as those we noted in Southeast Alaska, although the relative abundances of each differed considerably (Sinclair and Zeppelin, 2002; Trites et al., 2007). The most common prey reported in the Gulf of Alaska in order of importance were pollock, salmon, Pacific cod, arrowtooth flounder, sand lance, herring, and Irish lords (*Hemilepidotus* sp.). Further west in the Aleutian Islands, however, Atka mackerel, salmon, cephalopods, Pacific cod, Irish lords, and pollock dominated the sea lion diet.

It is unclear what role pollock and Atka mackerel stocks alone have played in the different trajectories of Steller sea lion populations. Pollock were consumed in the Kodiak area—both prior to what was thought to be the beginning of the decline (Pitcher, 1981) and after the decline was under way (Calkins and Goodwin¹). Calkins and Goodwin¹ noted that although sea lions ate more pollock in the Kodiak area after their decline in terms of frequency of occurrence, the pollock they ate were significantly smaller after the decline began. No similar data are available for Southeast Alaska.

Since the mid 1970s, pollock has been one of the most dominant species in the Bering Sea and Gulf of Alaska ecosystems (Livingston, 1993; Trites et al., 1999; Conners et al., 2002). Unfortunately, little is known about the relative importance of pollock in the Southeast Alaska ecosystem. Pollock have been little exploited, and relatively little is known about their distribution in Southeast Alaska. Surveys conducted during 1950–62 (Alverson et al., 1964) and again during 1976–77 (Parks and Zenger, 1978) caught 64–129 lbs of pollock per hour in select areas of Southeast Alaska using a 400-mesh eastern otter trawl. The 1950–1962 surveys covered only outside waters from Hazy Islands to Dixon Entrance, whereas the later surveys were distributed throughout both inside and outside waters. Parks and Zenger (1978) estimated pollock biomass in Frederick Sound at 0.94 t/nmi². A more recent unpublished estimate indicates that the biomass may have been as much as seven times this level in Frederick Sound in 2001 (Sigler³). Thus, pollock would appear to be an important species in the ecosystem within some areas of Southeast Alaska.

The most striking difference between the diets of Steller sea lions in the different regions of Alaska is the diversity of prey consumed. Steller sea lions feed-

³ M. Sigler. 2004. Personal commun. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Auke Bay Lab, 11305 Glacier Highway, Juneau, AK, 99801.

ing in the Gulf of Alaska and Aleutian Islands during summer had diversity indices of 2–3, compared to 5.3 in Southeast Alaska (Fig. 5, Merrick et al., 1997; Sinclair and Zeppelin, 2002). Summer diets were dominated in the Aleutian Islands by a single species (Atka mackerel) and there were small amounts of other prey in the diet. In the Gulf of Alaska, the dominant prey was pollock, followed by salmon (Sinclair and Zeppelin, 2002). Dietary diversity remained low in the Gulf and Aleutian Islands from summer to winter (Sinclair and Zeppelin, 2002), but dropped in Southeast Alaska from 5.3 to 4.1 (Fig. 5). Winter diets in Southeast Alaska were dominated by pollock. However, the average scat from Southeast Alaska contained at least two prey species. In other words, pollock was rarely consumed alone and, when consumed, was usually accompanied by at least one other species type, such as herring, salmon, sand lance, flatfish, or skates (Figs. 2 and 6).

The inclusion of our data from Southeast Alaska with those from Merrick et al. (1997) provided the same conclusion, namely that the numbers of sea lions declined more slowly and even increased as diversity of diet increased (Fig. 9). Steller sea lions that consumed the least diverse diet experienced the greatest population declines. However, it is not clear whether diet diversity is a proxy for energy content of the sea lion diet as suggested by Winship and Trites (2003), or whether it captures some other biologically meaningful measure of nutrition. Nor is it clear whether the diet diversity index reflects depths of nearest ocean passes to rookeries (with diet diversity increasing with shallower depths; Sinclair et al., 2005), or whether it could be a relative measure of prey distribution and density.

The relative importance of pollock in the diet of Steller sea lions in Southeast Alaska was not expected. However, pollock is not as dominant in the sea lion diet in Southeast Alaska as it is in other regions, and appears to usually be accompanied by other types of energy-rich prey (Fig. 4). It may be easier for sea lions with a more diverse or energy-rich diet to obtain sufficient prey to meet their energy requirements (Trites, 2003; Rosen and Trites, 2004; Trites et al., 2006). They may also be less sensitive to changes in overall prey abundance and may spend less time foraging under risk of predation.

The increase in Steller sea lion numbers in Southeast Alaska since the 1970s contrasts sharply with the declines observed in the Gulf of Alaska. The difference between the diets of Steller sea lions in the two regions is one possible explanation underlying the population trends. Stomach samples collected in the Bering Sea and Gulf of Alaska before the population decline (1950s–mid-1970s) indicate that their diet might have once resembled that of sea lions in Southeast Alaska during the 1990s (Alverson, 1992; Merrick et al., 1997; Sinclair and Zeppelin, 2002). However, the small number of stomachs sampled and the nonstandard methods used to collect them make it difficult to compare pre- and post-decline periods over broad areas. A change in diet during the population decline

may be related to large-scale changes in oceanographic conditions (regime shifts) that may have affected the relative abundances of different suites of species (Wilderbuer et al., 2002; King, 2005; Trites et al., 2007). In terms of oceanic regimes, the marine ecosystems of the eastern North Pacific appear to group into two broad domains (California to Southeast Alaska, and the Gulf of Alaska to western Aleutian Islands) that are out of phase with each other as they alternate between anomalous warm and cool states (regimes). Finer-scale analyses should be undertaken to determine how the declines and increases of different prey and predator species line up in time and space with changes in oceanographic events.

Conclusions

A comparison of our dietary data with dietary data collected from other regions of Alaska indicated that Steller sea lions consumed a relatively similar suite of schooling species, most notably pollock, salmon, herring, sand lance, rockfish, and squid. However, in terms of frequency of occurrence, there were marked differences between Southeast Alaska during the 1990s and regions where sea lions have declined. Diets in Southeast Alaska were more diverse and may have had a higher energy content overall. Pollock is part of a normal sea lion diet but is less dominant in Southeast Alaska than in the Gulf of Alaska and Bering Sea where population declines occurred. The difference in diets between the regions is potentially a useful clue for determining why population trends of Steller sea lions have diverged in Alaska. This difference in diets also underlines the overall importance of continuing to assess and monitor sea lion diets.

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