Diets of Mature Male and Female Steller Sea Lions (*Eumetopias jubatus*) Differ and Cannot Be Used as Proxies for Each Other

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Abstract

Disturbance of otariid breeding sites (rookeries) to determine diet from fecal remains (scats) could be eliminated if the diets of males using adjoining bachelor haulouts could be used as a proxy for diets of breeding females. We collected scats from sexually mature Steller sea lions (*Eumetopias jubatus*) at one male resting site (haulout) and three female dominated breeding sites (rookeries) at Forrester Island, southeast Alaska (June and July, 1994 to 1999) to test whether the diets of bachelor bulls differed from that of breeding females. Female diets were fairly evenly distributed between gadids, salmon, and small oily fishes (forage fish) and contained lesser amounts of rockfish, flatfish, cephalopods, and other fishes. The female diet did not differ significantly between the three rookeries, but it did differ significantly from that of males. Males consumed significantly fewer salmon and more pollock, flatfish, and rockfish compared to females. The males also consumed larger pollock compared to females. These dietary differences may reflect a sex-specific difference in foraging areas or differences in hunting abilities related to the disparity in physical sizes of males and females. The similarity of the female diets between rookeries suggests that female diets can be determined from samples collected at a single site within a rookery complex. Unfortunately, summer diets of breeding females cannot be ascertained from hard parts contained in the scats of mature male Steller sea lions.

Key Words: Steller sea lion, *Eumetopias jubatus*, prey, diet, size, diet diversity, diet composition

Introduction

Diet is one of the fundamental pieces of information needed to conserve and manage wildlife populations. This is particularly true for Steller sea lions (*Eumetopias jubatus*), which declined to low numbers in the Gulf of Alaska and Aleutian Islands through the 1980s and 1990s (Trites & Larkin, 1996; Winship & Trites, 2006). The reason why Steller sea lions declined is not yet known (NMFS, 1992; Loughlin, 1998), but there is speculation that it could be related to a change in the quality and quantity of prey available to them (Alverson, 1992; Alaska Sea Grant, 1993; Rosen & Trites, 2000; DeMaster & Atkinson, 2002; Trites & Donnelly, 2003; Winship & Trites, 2003; Rosen & Trites, 2005). Unfortunately, information about what Steller sea lions ate in western Alaska prior to their population decline is limited.

Historically, diets were determined by shooting Steller sea lions and examining their stomach contents (e.g., Pitcher, 1981; Calkins, 1998; Goto & Shimazaki, 1998). Killing and recovering sea lions was a labor intensive and time consuming process that resulted in small sample sizes. Today, dietary studies have moved away from identifying prey found in stomachs toward identifying the hard parts of prey that are found in feces (scats) collected on land (Merrick et al., 1997; Sinclair & Zeppelin, 2002; Trites et al., 2007). The greatest advantage of scats over stomachs is that animals do not have to be destroyed, and large sample sizes can be gathered. However, collecting Steller sea lion scats usually requires displacing the animals that are on shore.

Most of the recognized Steller sea lion rookeries are collections of distinct breeding groups on different beaches or offshore rocks and islands. The rookeries consist of mature bulls holding territories and large numbers of mature females with their newborn pups or dependent young from the previous year (juveniles). The bachelor haulouts that adjoin rookeries often consist of sexually mature males (bulls) that are not holding territories on the rookery either because they are too old,

inexperienced, or of insufficient body size. Unlike breeding males on the rookery, bachelor bulls freely associate with one another and do not appear to be territorial (pers. obs.). Their haulouts are typically located adjacent to the breeding sites and differ from other summer haulouts used by a mixture of males and females of different age classes.

Knowing what Steller sea lions eat may be one of the most important pieces of information needed to assist with their recovery and to resolve why their populations declined (NMFS, 1992). It is equally important to minimize the amount of disturbance researchers inflict on the animals to obtain this information (NMFS, 2007). Outside of the summer breeding season, Steller sea lions readily enter the water when disturbed by humans, eagles, or even other sea lions (Kucey & Trites, 2006). However, Steller sea lions at rookeries are more reluctant to leave their pups (females) or territories (males) when disturbed during the breeding season.

We sought to develop a scat-sampling protocol that would minimize disturbance to Steller sea lions during the breeding season yet would yield accurate data about what they eat. We wanted to verify two things. The first was that the diets of breeding animals (females) using adjacent islands and beaches did not differ from each other. If they did not differ, it would mean that scats could be collected from one of the breeding groups to determine the diet of all breeding females, and that different groups could be sampled in different years to reduce overall disturbance of the breeding population. Our second objective was to test whether the diet of bachelor bulls was the same as that of the nearby breeding population (females). If diets of the two groups were similar, it would mean that the diets of breeding Steller sea lions could be determined in future years at no cost to the rookery populations and at a minimum cost to the bulls resting on the nearby haulouts.

Materials and Methods

Our study was conducted at Forrester Island in southeast Alaska (Figure 1) during the 1994 through 1999 breeding seasons. This rookery complex is currently home to the largest breeding group of Steller sea lions in the world and is composed of a bachelor haulout (West Rocks) and seven major breeding groups on offshore rocks and islands (of which the three most significant are North Rocks, Sea Lion Rocks, and Cape Horn Rocks).

We collected scats opportunistically from mid-June to the first week of July when rookeries were disturbed to count pups or for other research purposes. However, we deliberately disturbed males to collect scats from the bachelor haulout. Most if
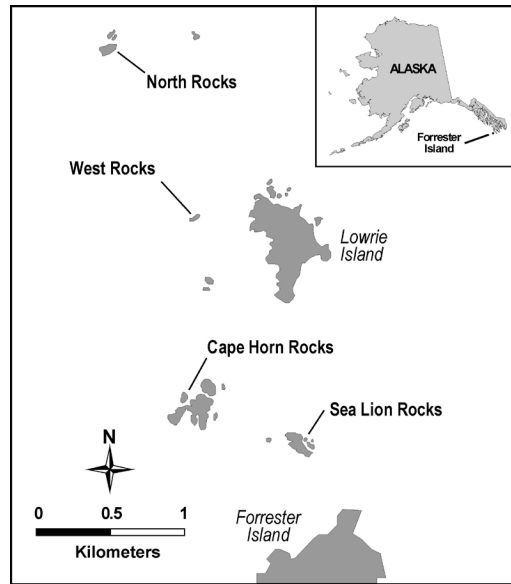

Figure 1. Major breeding concentrations of Steller sea lions making up the Forrester Island complex of rookeries in southeast Alaska; nonbreeding males only occurred on West Rocks.

not all of the scats from the rookeries were from adult females given that breeding males fast and dependent juveniles are rarely present. Each scat was placed in a zip-lock plastic bag and was frozen in a 5-gallon plastic bucket prior to shipping to the Food and Energy Consumption Laboratory at the Vancouver Aquarium for cleaning. Each scat was transferred to a plastic jar and soaked in water for about a week. Periodic shaking of the jars ensured that the scats broke down to 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 & Olesiuk, 1990) before the remaining sample was washed in a fine mesh screen (mesh size 0.5 mm). Pacific IDentifications Inc. (Victoria, BC) identified the cleaned and dried hard parts using a reference collection of prey species skeletons, noting the types of hard parts present, the species from which they came, the estimated size of the prey by species, and the minimum number of individuals present (all species combined based on maximum paired numbers of eye lenses or other unique identifiable structures).

We grouped the identified species of prey into eight categories for statistical analysis: (1) forage fish (small schooling oily fishes): capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasi*), eulachon (*Thaleichthys pacificus*), Pacific sandlance (*Ammodytes hexapterus*), and smelt (*smelt* spp.); (2) salmon (*Oncorhynchus* spp.); (3) gadids:

walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific hake (*Merluccius productus*), and unidentified gadids; (4) rockfish (*Sebastes* spp.); (5) flatfish: arrowtooth flounder (*Atheresthes stommias*), rock sole (*Lepidopsetta bilineatus*), halibut (*Hippoglossus stenolepis*), and other pleuronectids; (6) cephalopods: squid and octopus; (7) hexagramids: Atka mackerel (*Pleurogrammus monopterygius*) and lingcod (*Ophiodon elongatus*); and (8) other prey: skates (*Raja* spp.), dogfish (*Squalus acanthias*), lamprey (*Lampetra* sp.), sculpins (Cottidae), and lower numbers of miscellaneous species. The prey species were grouped by prevalence in the diet and by similarities in behavior, taxonomy, and nutritional value.

Scats that only contained prey that were too far digested to be identified were excluded from further analyses, while 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 herring and sandlance was scored as having a single occurrence of forage fish.

The relative importance of prey in the diet was quantified as "simple" and "split-sample" frequency of occurrences (Olesiuk et al., 1990). The simple frequency (%) of occurrence indicates what proportion of scats contained any particular prey type. They do not sum up to 100%. For example, 80% of the scats examined may contain gadids, and 50% may contain forage fish—that is, some scats contained both prey types, while 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)—estimated the proportion of the overall diet made up of any single prey type. These proportions will sum to 100%. For example, the average diet from the previous example would consist of 65% gadids and 35% forage fish. This split-sample method assumes that the scat contains remains from all prey consumed in the previous meal and that the prey was consumed in equal volumes.

Diet diversity was calculated for the eight prey groups described above using the Shannon-Wiener species diversity index (Ricklefs, 1980) as applied by Merrick et al. (1997). This index yields a value between 1 and 8—with a value of 1 indicating that only one of the eight groups was consumed, and a value of 8 indicating that all eight were equally consumed.

Six species (pollock, herring, sandlance, rockfish, salmon, and arrowtooth flounder) were consumed in high enough numbers to estimate their size (by comparing the sizes of hard parts found in the scat with those of a reference skeleton collection maintained by Pacific IDentifications Inc.). Estimated sizes were grouped into eight size classes (Table 1). For each size class, we multiplied the estimated number of individuals in the scat by the median length of each class to determine the mean length of species consumed.

We assumed that each scat represented an independent sample of prey remains and that the presence or absence of prey species within each scat was independent of each other. We thus performed contingency table analyses (Pearson χ^2, $\alpha = 0.05$) on the simple frequencies of occurrences to test whether the distributions of prey groups (that occurred at frequencies of $> 5\%$, max $n = 8$ groups) were homogeneous among sites (rookeries and haulouts) and across time (years). Average sizes of prey consumed by males and females, the size of their scats, and the number of categories of prey each consumed (i.e., the number of prey groups per scat) were compared using nonparametric tests (Mann-Whitney U, $\alpha = 0.05$).

Table 1. Eight size classes (with corresponding ranges and median fork lengths in cm) used to classify six species of fish recovered from Steller sea lion scats.

Size class	Pollock		Herring		Sandlance		Rockfish sp.		Salmon sp.		Arrowtooth flounder	
	Range	Med.	Range	Med.	Range	Med.	Range	Med.	Range	Med.	Range	Med.
1	5-7	6.0	5-7	6.0	5-7	6.0	5-7	6.0	5-15	10.0	5-7	6.0
2	8-11	9.5	8-10	9.0	8-10	9.0	8-15	11.5	16-24	20.0	8-15	11.5
3	12-19	15.5	11-15	13.0	11-15	13.0	16-30	23.0	25-34	29.5	16-24	20.0
4	12-29	20.5	11-29	20.0	11-19	15.0	16-49	32.5	25-59	42.0	16-40	28.0
5	20-29	24.5	16-29	22.5	16-19	17.5	31-49	40.0	35-59	47.0	25-40	32.5
6	30-69	49.5	16-40	28.0	16-24	20.0	31-69	50.0	35-90	62.5	25-60	42.5
7	--	--	30-40	35.0	20-24	22.0	50-69	59.5	60-90	75.0	41-60	50.5
8	--	--	40-45	42.5	25-27	26.0	70-90	80.0	91-130	110.5	61-80	70.5

Results

A total of 780 scats were collected at Forrester Island from 1994 to 1999 of which 5.9% contained prey that could not be identified with certainty (two scats had no remains and 44 contained unidentifiable remains). Analysis was thus conducted on the remains found in 734 scats (264 from the male haulout and 470 from the three rookeries). Sample sizes were sufficient for statistical analysis (Trites & Joy, 2005) and were fairly well distributed between years and sites, except in 1996 and 1999 when few samples were obtained from rookeries, and in 1994 and 1996 when no samples were collected from the male haulout (Figure 2).

A total of 43 species of prey were identified from all of the scats we examined. The most frequently recovered prey of adult females in order of importance (i.e., with a frequency of occurrence > 25%; Figure 3) were walleye pollock, salmon, Pacific herring, sandlance, rockfish, and arrowtooth flounder. For males, the most common prey were pollock, rockfish, flatfish, and herring (Figure 3). Grouping the prey into six categories (forage fish, salmon, gadids, rockfish, flatfish, and other), we found no significant differences between the diets of females at the three rookeries in all years, except in 1996 (Table 2). The 1996 result is suspect, however, due to the small number of scats collected during this year ($n =$
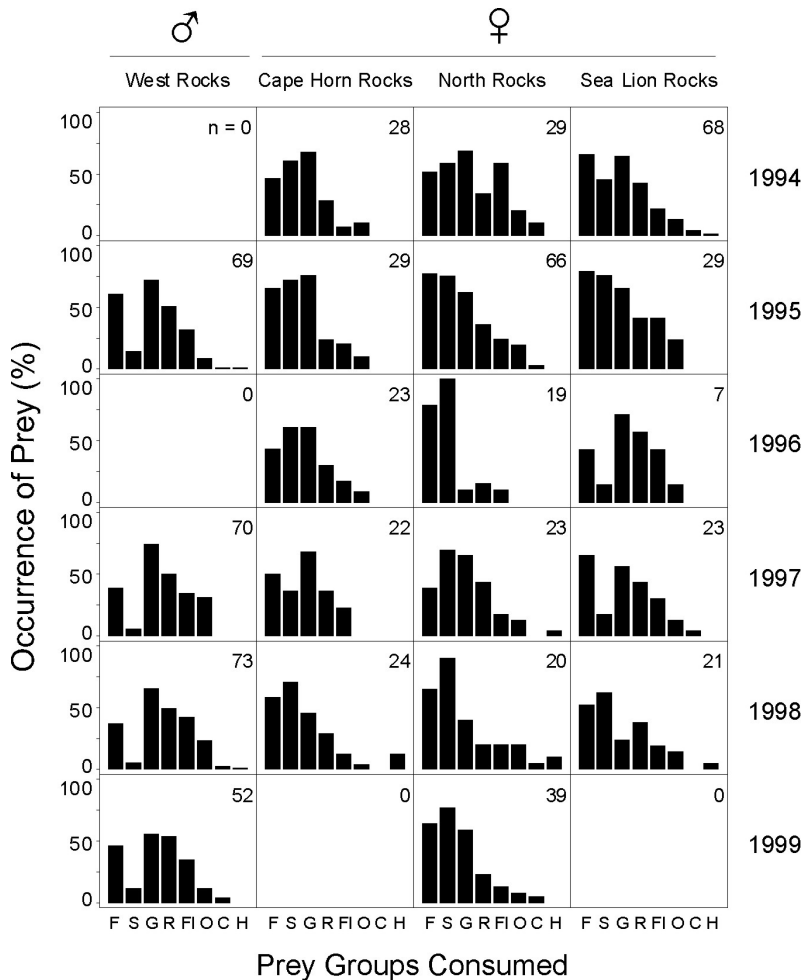

Figure 2. Frequency of occurrence of eight groups of prey contained in scats collected during summers (1994-1999) from the male haulout (West Rocks) and from three major breeding areas making up the Forrester Island rookery complex (Cape Horn Rocks, North Rocks, and Sea Lion Rocks); species groups included forage fish (F), salmon (S), gadids (G), rockfish (R), flatfish (Fl), other species (O), cephalopods (C), and hexagramids (H). Data were pooled across months (June-July). Sample sizes shown in each panel indicate numbers of scats collected.
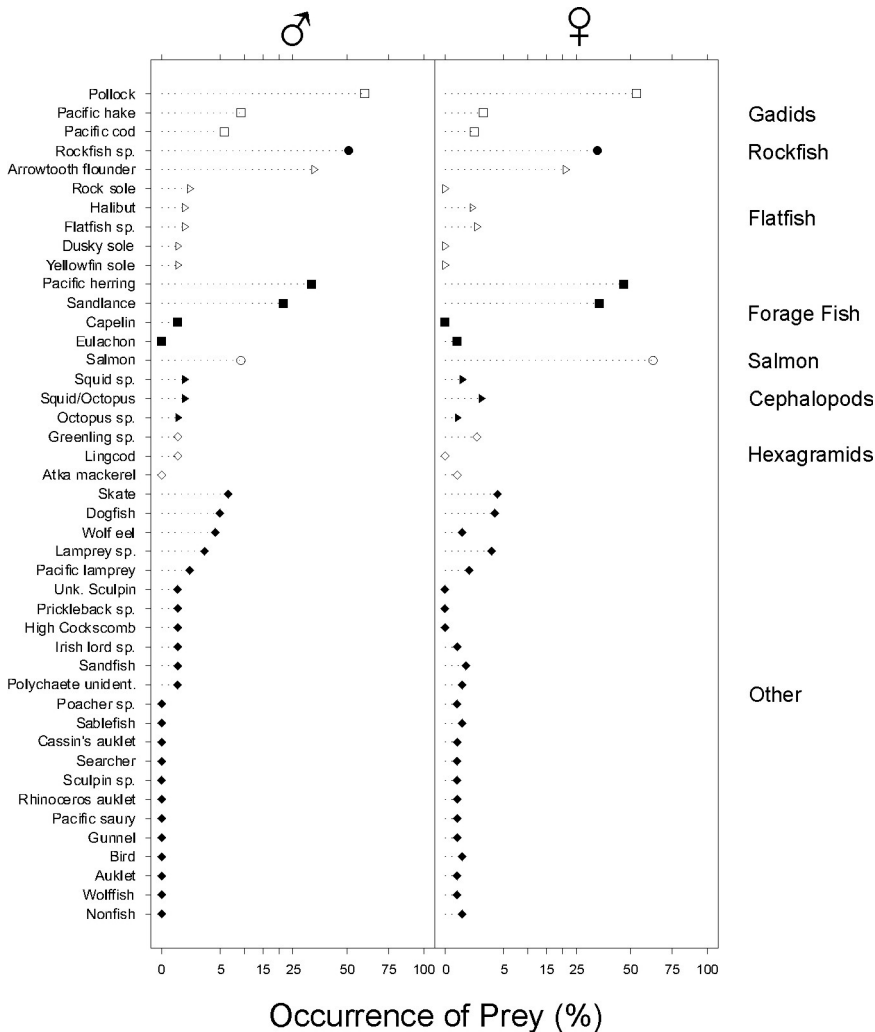
Figure 3. Frequency of occurrence of individual prey species in scats from males (*n* = 264 scats) and females (*n* = 470 scats) at Forrester Island in summer (June-July, 1994-1999); data were pooled across months, years, and rookery sites. The X-axes were scaled (square-root transformation) to improve the visual resolution of the lower frequencies of occurrences.

49) compared to all other years (when the average number of scats collected was 95). We therefore concluded that there were no significant differences between the diets of females using the three breeding sites at Forrester Island. Nor did we find a significant difference in female diets over time (1994 through 1999; Table 2). Male diets also appeared to remain relatively constant over the sampled years (Table 2; Figure 2). However, male and female diets did differ significantly from one another (Table 2; Figure 4).

Based on the presence and absence of prey in the scat, females consumed 22% forage fish, 28% salmon, 24% gadids, 13% rockfish, 7% flatfish, 4% other fishes, 1% cephalopods, and

< 1% hexagramids (split-sample-frequency-of-occurrence estimates). In contrast, males consumed 17% forage fish, 3% salmon, 33% gadids, 25% rockfish, 15% flatfish, 7% other fishes, 1% cephalopods, and < 1% hexagramids. Thus, the major differences between male and female diets was that females consumed more salmon and forage fish, compared to males who ate more gadids, flatfish, and rockfish (Figure 4).

The average size of male scats (315.7 ml ± 202.9 ml SD, *n* = 264, range = 40 to 1,000 ml) was significantly larger than female scats (252.6 ml ± 169.1 ml SD, *n* = 470, range = 5 to 1,180 ml) (Mann-Whitney U = 4.1, *p* < 0.001; Figure 5). However, the average individual male scat

Table 2. Contingency analyses tests of homogeneity of diet (n = six prey groups) by year of collection and haulout (H) and rookery (R) sites showing Pearson χ^2, degrees of freedom (df), and statistical significance (p); the rookeries compared included North Rocks (N), Sea Lion Rocks (S), and Cape Horn Rocks (C). Prey groups included forage fish, salmon, gadids, rockfish, flatfish, and other species. Cephalopods and hexagramids occurred at < 5% frequency of occurrence and were excluded from the analyses.

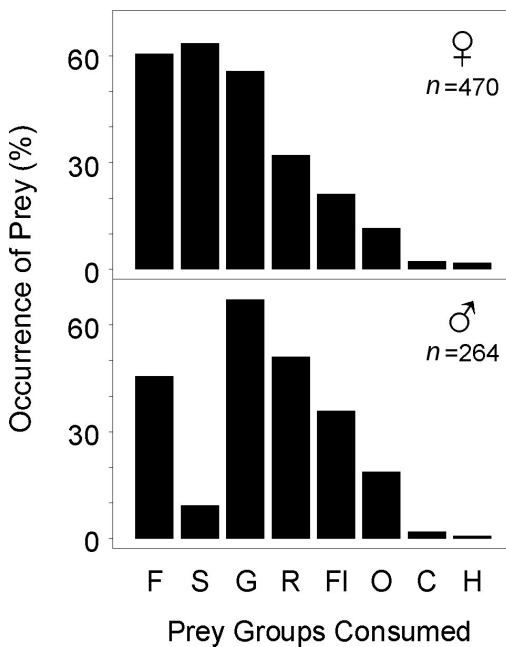| Year	Sites	χ^2	df	p
1994	N•S•C	17.1	10	0.07
1995	N•S•C	5.2	10	0.88
1996	N•S•C	23.8	10	0.01
1997	N•S•C	12.7	10	0.24
1998	N•S•C	5.9	10	0.82
1999	N•S	6.6	5	0.25
1994-1999	R	30.3	25	0.21
1995, 1997-1999	H	23.3	15	0.08
1995	R•H	35.0	5	<0.001
1997	R•H	31.2	5	<0.001
1998	R•H	64.5	5	<0.001
1999	R•H	32.2	5	<0.001

Figure 4. Frequency of occurrence of eight groups of prey from mature male and female Steller sea lions at Forrester Island; species groups included forage fish (F), salmon (S), gadids (G), rockfish (R), flatfish (Fl), other species (O), cephalopods (C), and hexagramids (H). Data were pooled across months (June-July) and rookery sites (Cape Horn Rocks, North Rocks, and Sea Lion Rocks), and were averaged across years (1994-1999). Sample sizes indicate numbers of scats collected.

contained prey remains from a mean of 2.31 prey groups (of a possible maximum of eight prey categories), while female scats contained a mean of 2.58 prey groups (Mann-Whitney U = 2.6, p = 0.001). The relationship between scat volume and number of prey groups identified was nonlinear (Figure 5), suggesting that bigger scats tended to reflect a greater number and total mass of consumed prey groups. The larger male scats contained an average of 2.95 fish, while those of the smaller female scats had 4.82 fish (minimum numbers of individuals). Diet diversity did not differ significantly between males (5.11) and females (5.35) (on a scale of 1 to 8 prey categories), however.

With the exception of pollock, males and females ate about the same size fish (i.e., herring, sandlance, salmon, rockfish, and arrowtooth flounder; Figure 6). For example, herring eaten by males (mean = 28.0 cm) did not differ significantly in size from those eaten by females (mean = 28.8 cm) (Mann-Whitney U = 0.9, p = 0.36); however, most of the pollock eaten by males (mean = 46.0 cm) were significantly larger than those consumed by females (mean = 39.8 cm) (Mann-Whitney U = 5.9, p < 0.001). Overall, the lengths of pollock, which were estimated by comparing the sizes of recovered hard parts with skeletal reference collections, were similar to those estimated from a regression analysis of measured hard parts (Tollit et al., 2004).
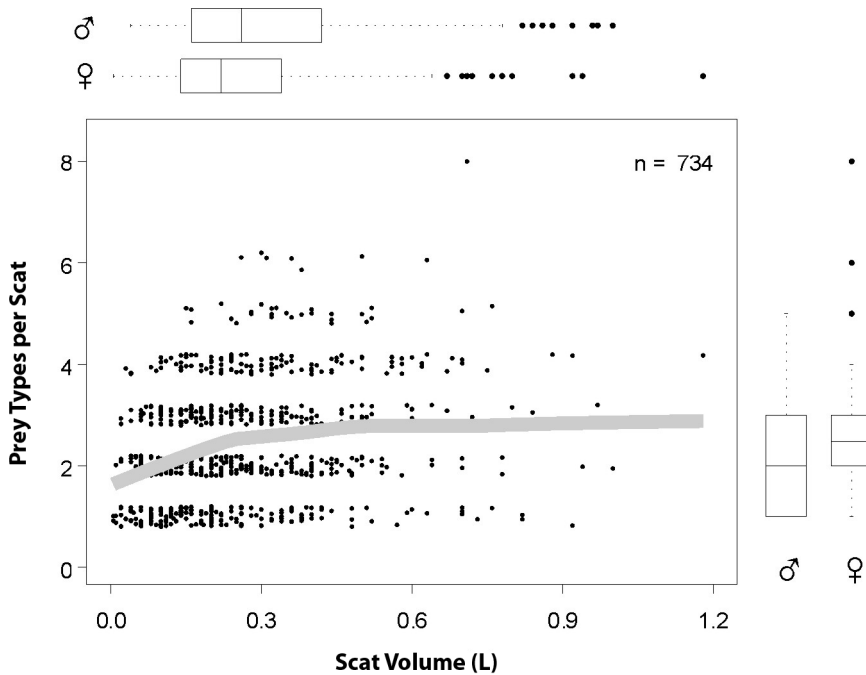
Figure 5. Relationship between the size of a scat (volume) and the number of prey types it contained (max = 8); the plotted number of prey types per scat were jittered by adding random variation (uniform distribution, ± 0.2) to each value to improve the visual representation of data. The locally weighted smoothed curve (lowess, F = 0.67) was fit to the nonjittered data. Box plots in the margins show the distribution of prey types and volumes of scats collected from male (*n* = 264) and female (*n* = 470) Steller sea lions.
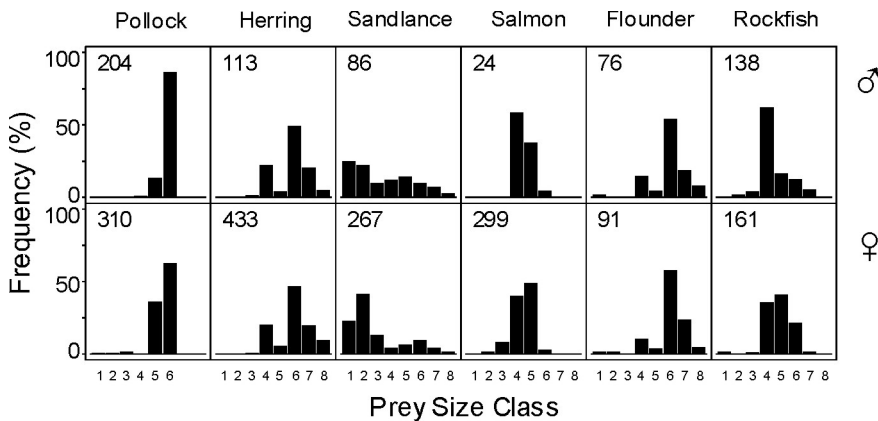
Figure 6. Size classes of the six most common prey species consumed by male and female Steller sea lions at Forrester Island during summer (June-July, 1994-1999); size classes correspond to those listed in Table 1. Sample sizes indicate the number of fish whose sizes were estimated from bony remains contained in the sea lion scats.

Discussion

Our study was motivated by a desire to reduce the level of disturbance associated with collecting scats from Steller sea lion rookeries. To that end, we found that it is not necessary to sample scats from all of the breeding sites that make up the Forrester Island complex because females using these rookeries all share the same diet. Unfortunately, the male diet differed from that of breeding females and cannot be used as a proxy for female diet at Forrester Island.

Sex-specific differences in diet have been reported for at least two other sexually dimorphic pinnipeds: (1) South American sea lions (*Otaria flavescens*) and (2) grey seals (*Halichoerus grypus*) (Alonso et al., 2000; Beck et al., 2005; Tucker et al., 2007). Such differences may reflect differential ecological constraints associated with dimorphism, polygyny, and life history strategies, but they are not understood. Sex-specific differences have also been noted in the feeding behaviors of other species of mammals as well as birds, and are thought to be related to sexual size dimorphism, reduced intraspecific competition for food, and/or differential reproductive roles (e.g., Clutton-Brock et al., 1982; Petit et al., 1990; Ginnett & Demment, 1997; Clarke et al., 1998).

Among pinnipeds, male and female grey seals, northern fur seals (*Callorhinus ursinus*), and northern elephant seals (*Mirounga angustirostris*) appear to forage in different areas (LeBoeuf et al., 2000; Robson et al., 2004; Sterling & Ream, 2004; Breed et al., 2006), which presumably reduces intraspecific competition. Northern elephant seals and grey seals have also been shown to have sex-specific dive patterns that may reflect different strategies for storing reproductive energy (LeBoeuf et al., 2000; Beck et al., 2003a, 2003b). Male grey seals were reported to dive deeper, but they had shorter dives and spent less time at depth than females. They also dove consistently throughout the day unlike females that had strong diurnal patterns (Beck et al., 2003b).

In the case of Steller sea lions, a possible explanation for the observed dietary differences between males and females is that males require a different mix of fish to meet their higher energetic needs. Energetic modeling suggests that a mature male Steller sea lion requires about 25 to 40 kg of prey per day compared to 10 to 20 kg for a mature female (depending on the season and assuming they consumed the same mixed diet; Winship & Trites, 2003). Males might be able to consistently capture higher numbers of bottom fish (pollock, flatfish, and rockfish), but they would acquire fewer calories per unit weight of prey than females consuming herring, sandlance, and salmon. Conceivably, the larger males might also have higher gut capacities to digest larger quantities of lower quality foods than the smaller females and could therefore be less selective about what they eat (e.g., Kastelein et al., 1990; Mysterud, 2000).

Another possibility to account for the dietary differences of Steller sea lions is that morphometric differences between males and females affects their ability to capture different species of prey (mature males are about 2.5 times larger than mature females; Winship et al., 2001). Salmon, for example, may be too fast or agile to be captured efficiently by large males. Other possibilities are that males can dive deeper than females and have access to different mixes of fish, or that there are sex-specific differences in digestion rates (including diet composition-induced differences). Unfortunately, no data are available to test these hypotheses.

Satellite tracking of lactating female Steller sea lions captured at Cape Horn Rocks and Sea Lion Rocks has shown that they consistently traveled and fed over the continental shelf north of Forrester Island (Swain, 1996; Andrews et al., 2002). This may explain our finding that diets of females from the three rookeries were similar. The finding of Norcross et al. (2000) that fish densities were highest north of the Forrester Island rookeries is presumably the reason why the females go there. Males may travel to deeper waters along the continental shelf, but their foraging ecology has never been studied.

The need to accurately determine what Steller sea lions eat must be balanced with the cost of obtaining this information to ensure the long-term conservation of the species (NMFS, 2007). Our findings that females using the rookeries at Forrester Island had similar diets and that their diets differed from males may apply to other rookery complexes and other populations of mature male and female Steller sea lions, but other such comparisons between sites and sexes have not been undertaken yet. Efforts should therefore be made to compare dietary collections from other rookeries and haulouts in Alaska to determine the minimum number of rookeries and haulouts that need to be sampled to accurately quantify diet.

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