Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples

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Abstract—Marine mammal diet is typically characterized by identifying fish otoliths and cephalopod beaks retrieved from stomachs and fecal material (scats). The use and applicability of these techniques has been the matter of some debate given inherent biases associated with the method. Recent attempts to identify prey using skeletal remains in addition to beaks and otoliths are an improvement; however, difficulties incorporating these data into quantitative analyses have limited results for descriptive analyses such as frequency of occurrence. We attempted to characterize harbor seal (*Phoca vitulina*) diet in an area where seals co-occur with several salmon species, some endangered and all managed by state or federal agencies, or both. Although diet was extremely variable within sampling date, season, year, and between years, the frequency and number of individual prey were at least two times greater for most taxa when prey structures in addition to otoliths were identified. Estimating prey mass in addition to frequency and number resulted in an extremely different relative importance of prey in harbor seal diet. These data analyses are a necessary step in generating estimates of the size, total number, and annual biomass of a prey species eaten by pinnipeds for inclusion in fisheries management plans.

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Increases in marine mammal populations in Washington and Oregon have coincided with decreases in wild salmon populations in these and other western states. Recently, several salmon stocks in the western U.S. have been listed as threatened, endangered, or are under status review. These include coastal Oregon coho (*Onchorhyncus kisutch*), upper Columbia River steelhead (*O. mykiss*), and Snake River spring and fall chinook (*O. tshawytscha*), steelhead, and sockeye salmon (*O. nerka*; NMFS, 1997). Salmon often co-occur with marine mammals and predation may substantially reduce fish populations (Gearin et al., 1986). In these circumstances, an understanding of pinniped diet becomes necessary for the management of endangered fish populations. In 1994, the National Marine Mammal Laboratory began a project to quantify harbor seal (*Phoca vitulina*) predation on salmon in the lower Columbia River and to incorporate marine mammals in salmonid population models. Harbor seals are the most abundant pinniped in the lower river and annual maximum counts can exceed 2000 on the largest haul-out site, a tidal sandbar adjacent to Astoria, Oregon.

Pinniped prey are typically identified from fish sagittae (otoliths) recovered from fecal material (scat) and stomach contents (Brown, 1980; Harvey, 1989; Peirce and Boyle, 1991; Ochoa-Acuña and Francis, 1995; Beach et al.[1]). These methods yield biased results because of partial or complete digestion of otoliths and because of greater probabilities of recovering otoliths from larger individuals and species with robust otoliths and of identifying otoliths of species with distinctive morphological characteristics (Harvey, 1989; Gates and Cheal, 1992; Cottrell et al., 1996; Tollit et al., 1997; Bowen, 2000). Estimates of harbor seal predation on adult salmonids are particularly poor due to extremely low recovery (because the otoliths are small and fragile) and because harbor seals may not completely ingest large prey and thus otoliths may not be ingested (Pitcher, 1980; Harvey, 1989; Boyle et al., 1990; Harvey and Antonelis, 1994; Cottrell et al., 1996; Riemer and Brown, 1997).

We describe harbor seal diet on the lower Columbia River during spring, summer, and fall from 1) otoliths and 2) other skeletal elements (cranial bones, vertebrae, teeth, gill rakers, etc.) to examine potential differences in the diet characterized by the two methods. In previous studies, identification of all

[1] Beach, R. J., A. C. Geiger, S. J. Jefferies, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982. NWAFC (Northwest Alaska Fisheries Science Center) processed rep. 85-03, 316 p. NWAFC, National Marine Fisheries Service, Seattle, WA.

skeletal elements resulted in at least two times greater frequency of occurrence of some prey taxa than frequencies exclusively derived from otoliths (Riemer and Brown, 1997; Boyle et al., 1990; Cottrell et al., 1996). For major prey taxa, we estimated frequency of occurrence and minimum number of individuals from fish otoliths and other skeletal remains recovered from scats and average mass from otoliths.

Methods

During 1995, 1996, and 1997, scats were collected from Desdemona Sands (river km 26, 123°52′W,46°13′N), the largest harbor seal haul-out site in the lower Columbia River (Huber[2]). Scats were collected intermittently during 1995. From March through August 1996 and from March through October 1997, we attempted to collect 50 harbor seal scats every two weeks at extreme low tides. This sampling period coincided with Columbia River runs of spring, summer, and fall chinook salmon. Scats were collected from haul-outs, and upon arrival at the laboratory were rinsed in nested sieves (2-mm, 1-mm, and 0.5-mm mesh width). All skeletal elements were recovered, dried, and stored in vials. Cephalopod remains were stored in 70% isopropyl or ethyl alcohol. Other invertebrate remains were relatively rare (≤2% frequency of occurrence) and their contribution to the diet was disregarded because of difficulties enumerating individuals and determining primary from secondary (prey within large, ingested fishes) prey. Otoliths were identified to lowest possible taxon, their anatomical location recorded (left or right side), and enumerated (number for left side and number for right side). Lengths of intact left or right otoliths were measured parallel to the sulcus to the nearest 0.1 mm with an ocular micrometer. Micrometer measurements were verified with hand-held calipers. Other skeletal structures (such as teeth, vertebrae, and cranial bones) were identified to lowest possible taxon by comparing prey remains to reference samples (NMML[3]).

Scat collections were divided into three seasons: spring (samples collected prior to 15 May), summer (samples collected from 15 May to 15 July), and fall (samples collected after 15 July). These dates distinguish runs of spring, summer, and fall chinook salmon crossing the Bonneville Dam (river km 235), less two weeks estimated for travel from the lower Columbia River (Fryer, 1998). For each season, harbor seal diet was described by frequency of occurrence (FO), minimum number of individuals (MNI), and average prey mass estimated from otoliths of all major prey taxa. Frequency of occurrence (FO) of prey taxon j in season k was defined as

$$FO_{jk} = \frac{\sum_{i=1}^{s_k} O_{ijk}}{s_k},$$

where O_{ijk} = a binary variate indicating presence (1) or absence (0) of taxon j in sample i in season k; and

s_k = the total number of scats containing identifiable prey remains in season k.

Rare prey taxa were grouped with similar taxa for analyses. Unknown prey remains that were clearly distinct from known taxa were considered "unidentified taxa" in samples containing "identified" hard parts. Scats containing skeletal remains considered "unidentifiable," i.e. extremely eroded bone or fragmented material, were excluded from analyses. The minimum number of individuals (MNI) was estimated from the greatest number of left or right otoliths and unique or paired bone structures and expressed within each season as total MNI or average MNI per scat (total MNI/number of scats collected). Presence of non-unique fish remains (non-unique vertebrae, gillrakers, teeth) constituted a single individual. For example, if a scat sample contained five left otoliths, three right otoliths, and six atlas or axis vertebrae of a prey taxon, the MNI was six. FO and MNI were calculated from otoliths and again from all prey remains. Prey masses were estimated for the three seasons from allometric relationships between otoliths and body size (Harvey et al., 2000; Table 1). If relationships were unavailable for a species, regressions generated for a similar species were used. Otolith lengths were multiplied by a species-specific correction factor when available or an average correction factor to account for reduction in length due to digestion (Harvey, 1989). All intact left or right otoliths of a prey taxa were measured, and estimated masses were averaged for each season.

Suitable morphometric regressions were not available for several salmon species or did not include juvenile fish; therefore, we generated regressions including subadult age classes specifically for our study. In addition to published regressions, relationships between salmon otoliths and fish mass used in this study were calculated from National Marine Mammal Laboratory reference samples, the private collections of Walker[4] and NRC[5] (Table 1). Because of the large discrepancy in masses of adult and juvenile salmonids, otoliths were identified to species and classified as adult or juvenile according to species-specific lengths estimated from regression equations. "Adults" described all returning upriver migrants, including reproductively mature individuals and jacks. "Juveniles" were seaward migrants and may have included two-year-old fish of some species (Groot and Margolis, 1991). *Onchorhyncus*

[2] Huber, H. R. 1997. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[3] NMML (National Marine Mammal Laboratory). 1997. Marine Mammal Prey Osteological Reference Collection. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[4] Walker, W. 1998. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[5] NRC (National Resources Consultants). 1998. Unpubl. data. Natural Resources Consultants, Inc., 4055 21st Ave. W, Suite 100, Seattle, WA 98119.

Table 1

Predicted standard length ($L=a+bx$; L=estimated standard length [cm], x=otolith length [mm]) and weight ($W=cL^d$; W=estimated weight [g], L=estimated standard length) of common harbor seal prey and sources of data. Calculations for groups of fish are based on species (in parentheses). Sockeye salmon calculations are based on regressions for silver salmon.

		Length		Weight		
Taxon	Species	*a*	*b*	*c*	*d*	Source
Ammodytidae	Pacific sand lance	0.727	0.137	0.0529	3.46	NMML[1]
Clupeidae	Pacific herring	–1.85	5.24	0.0044	3.398	Harvey et al., 2000.
	American shad	–11.08	11.46	0.0135	3.046	Harvey et al., 2000.
Cottidae	Pacific staghorn sculpin	–2.26	2.58	0.011	3.229	Harvey et al., 2000.
Embiotocidae	shiner surfperch	–0.52	1.74	0.01	3.515	Harvey et al., 2000.
Engraulidae	northern anchovy	0.85	2.28	0.0485	2.413	Harvey et al., 2000.
Gadidae	Pacific hake	0.96	2.04	0.0081	2.966	Harvey et al., 2000.
Gadidae	Pacific tomcod	–3.51	1.77	0.0064	3.191	Harvey et al., 2000.
Hexagrammidae	Hexagrammids (lingcod)	–6.03	8	0.0023	3.567	Harvey et al., 2000.
Osmeridae	whitebait smelt	3.02	2.11	0.0063	3.233	Harvey et al., 2000.
	eulachon	–2.7	4.71	0.0077	3.075	Harvey et al., 2000.
Pleuronectidae	Dover sole	12.23	2.75	0.0094	3.092	Harvey et al., 2000.
	English sole	–2.76	3.82	0.0163	2.939	Harvey et al., 2000.
	rex sole	–2.5	4.8	0.0238	2.692	Harvey et al., 2000.
	slender sole	1.08	3.37	0.0058	3.293	Harvey et al., 2000.
	starry flounder	0.23	3.35	0.0107	3.268	Harvey et al., 2000.
Salmonidae	chinook salmon	–10.4	6.73	0.0043	3.207	length: Walker[2]; weight: NRC[3]
	cutthroat trout	–91.2	89.3	0.0155	2.97	Walker[2]
	silver salmon	3.29	9.33	0.0103	3.092	length: NRC[3]; weight: Harvey et al., 2000.
	sockeye salmon (silver salmon)	3.29	9.33	0.0103	3.092	length: Walker[2]
	steelhead salmon	–32.43	14.77	0.0275	2.895	Harvey et al., 2000.
Scorpaenidae	rockfishes (black rockfish)	8.7	1.6	0.1225	2.499	Harvey et al., 2000.
Stichaeidae and Pholididae	gunnel and prickelback (wattled eelpout)	12.42	5.22	0.0007	3.483	Harvey et al., 2000.
	gunnel and prickelback (Pacific sand fish)	–4.57	6.06	0.0171	2.953	Harvey et al., 2000.

[1] NMML (National Marine Mammal Laboratory). 1997. Marine Mammal Prey Osteological Reference Collection. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA. 98115.

[2] Walker, W. 1998. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[3] NRC (National Resources Consultants, Inc.). 1998. Unpubl. data. National Resources Consultants, Inc. 4055 21st Ave. W, Suite 100, Seattle, WA, 98119.

clarki, O. kisutch, O. nerka, and *O. mykiss* less than 30 cm in length and *O. tshawytscha* less than 35 cm in length were considered seaward migrating juveniles (Groot and Margolis, 1991). All distinguishable salmon otoliths were identified to species and all identifications were verified by W. Walker.

Annual and seasonal variations in frequency of occurrence (FO) were examined with generalized linear models (Venables and Ripley, 1994). We limited our analyses to prey taxon with FO >5% during one or more seasons. Frequency of occurrence on each sampling date was modeled as a binomial random variable and for each prey taxon, we fitted five models: constant, season (S), year (Y), season+year ($S+Y$), and season+year with interactions ($S\times Y$). To account for overdispersion, we scaled Akaike's information criterion (AIC) using b=residual deviance/degrees of freedom from the $S\times Y$ model (Venables and Ripley, 1994). The model with the smallest scaled AIC was considered the best descriptor of seasonal and annual variation in FO.

Results

Over 1500 scats were collected from March 1995 through October 1997. Sample sizes varied among years and within season (Table 2). Frequency and number of indi-

Table 2

Sample collection dates, harbor seal scats with some identifiable prey remains, without any identifiable remains, and without remains for samples collected from Desdemona Sands 1995 through 1997. Spring (<15 May), summer (15 May to 15 July), and fall (>15 July) designate timing of chinook salmon runs on the Columbia River.

			Harbor seal scats		
Season	Collection date		With identifiable remains	Without identifiable remains	Without remains
Spring	5 Mar 1995		13	1	0
	5 Mar 1995		29	2	0
	14 Mar 1996		29	1	1
	21 Mar 1996		11	1	1
	10 Apr 1996		42	4	0
	2–8 May 1996		44	2	1
	11 Mar 1997		16	1	0
	26 Mar 1997		7	4	0
	10–11 Apr 1997		29	7	1
	15 Apr 1997		22	6	0
	28 Apr–1 May 1997		28	4	11
	9–10 May 1997		45	6	12
		Subtotal	315	39	27
Summer	18–19 May 1995		53	1	4
	14–16 Jun 1995		81	1	0
	28–29 Jun 1995		78	1	0
	14 Jul 1995		32	3	0
	30–31 May 1996		53	2	1
	18–19 Jun 1996		50	1	1
	2 Jul 1996		52	3	0
	27 May 1997		34	6	10
	6 Jun 1997		24	8	0
	23 Jun 1997		47	8	9
	8 Jul 1997		74	2	1
		Subtotal	578	36	26
Fall	15 Aug 1996		78	1	0
	29 Aug 1996		59	2	0
	22 Jul 1997		64	5	6
	4 Aug 1997		102	1	0
	19 Aug 1997		56	1	0
	3 Sep 1997		51	5	0
	16 Sep 1997		41	6	0
	16–17 Oct 1997		41	6	0
		Subtotal	492	27	6
	Total		1385	102	59

viduals consumed by harbor seals on the Columbia River were extremely variable, even among sample collections fewer than two weeks apart. Effort and sample sizes were unequal for season and years but we chose to include all data to better describe harbor seal diet. More than 45 prey taxa were described in 1385 samples with identifiable prey remains; however, most of the diet by number and frequency was composed of about 17 prey taxa (Table 3). Seasonal effects were important for 15 of 17 harbor seal prey with FO ≥5% (Table 3). Annual effects also were important for FO of lamprey (*Lampetra* spp.), Pacific hake (*Merluccius productus*), and northern anchovy (*Engraulis mordax*), and year-season interactions were included for three prey taxa (Table 3). All taxa had variances of FO greater than predicted by a binomial model (over-dispersion values, b>1; Table 3).

Table 3

Total minimum number of individuals (MNI), frequency of occurrence (FO), significant differences in frequency of occurrence of major prey taxa identified from all skeletal remains recovered from harbor seal scat (*S* indicates season, *Y* indicates year, *S*×*Y* indicates interaction, and N indicates no effects), and an estimate of over-dispersion of the binomial model (*b*). Only taxa with FO. >0.05 in at least one season were examined.

	MNI (all remains)			FO (all remains)				
Prey taxon	Spring	Summer	Fall	Spring	Summer	Fall	Effect	*b*
Pacific herring	168	511	141	0.36	0.57	0.22	*S*	8.4
Pacific staghorn sculpin	256	170	284	0.41	0.19	0.25	*S*×*Y*	2.4
Smelt species	133	204	625	0.28	0.18	0.35	*S*	6.2
Pacific tomcod	66	73	251	0.18	0.09	0.39	*S*	7.2
Lamprey species	109	204	41	0.26	0.25	0.06	*S*+*Y*	2.0
Starry flounder	136	105	160	0.30	0.14	0.12	*S*×*Y*	2.7
American shad	36	108	116	0.11	0.19	0.22	*N*	6.1
Other flatfish	102	129	132	0.20	0.12	0.18	*S*	2.2
Pacific hake	30	72	136	0.09	0.12	0.28	*S*+*Y*	4.0
Shiner surfperch	26	131	69	0.07	0.18	0.08	*S*	2.2
Gunnel and prickelback	47	55	30	0.15	0.08	0.06	*S*	3.0
Juvenile salmonids	92	71	30	0.19	0.05	0.05	*S*	3.2
Northern anchovy	3	63	290	0.01	0.06	0.19	*S*+*Y*	2.9
Adult salmonids	22	33	50	0.06	0.04	0.10	N	4.6
Peamouth chub	12	63	41	0.03	0.08	0.05	*S*×*Y*	2.4
Pacific sand lance	37	18	11	0.10	0.03	0.02	*S*	1.5
Rockfish species	23	14	18	0.07	0.02	0.03	*S*	1.5

The inclusion of all skeletal elements recovered from scat increased the MNI and FO of all harbor seal prey taxa (Table 4). The FO more than doubled for most taxa and usually was more affected by including all prey elements than was the average MNI (Table 4). We compared the MNI of several common harbor seal prey estimated from all structures to an estimate based on the number of recovered otoliths multiplied by a species-specific correction factor for recovery rate (accounting for complete digestion of the otolith; Harvey, 1989, Fig. 1). A value of 1.0 indicated that the same estimate was derived from both methods, whereas 0.5 indicated that the MNI estimated from all structures was twice the estimate from otoliths.

Seasonal variation was also apparent in estimated prey mass (Table 5). In some instances, estimates were based on very few otolith measurements, values were taken from the literature, or mass was averaged from other seasons when no intact otoliths were recovered (Table 5). Because some species were difficult to discern or regression relationships were unavailable, species were grouped by phylogeny or size similarities (Table 5). Smelts (Osmerids) were pooled by family and mass was estimated from whitebait smelt *(Allosmerus elongatus*), the most abundant species by distinguishable otoliths, and eulachon (*Thaleichthys pacificus*), although longfin smelt (*Spirinchus thaleichthys*) and surf smelt (*Hypomesus pretiosus*) were occasionally identified in harbor seal scats. Although smelt otoliths could be distinguished by species, smelt bone could not. Smelt mass estimates were based on eulachon (in their relative proportion) and whitebait smelt because although less common than the other three similar size species, eulachon were much larger. Masses of juvenile and adult salmonids were estimated separately for five species identified in harbor seal scat, with the exception of sockeye salmon, which was represented by one otolith from an adult fish. Mass for sockeye was based on regressions generated for silver salmon. Cutthroat (*Onchorhyncus clarki)* and steelhead salmon *(O. mykiss)* were not often distinguishable by otoliths, and mass estimates were based on steelhead because of their numerical dominance in the lower Columbia River. The sticheid-pholid group included fish from a variety of families: three spine stickleback (*Gasterosteus aculeatus*), snake prickleback (*Lumpenus sagitta*), high cockscomb (*Anoplarchus purpurescens*), wattled eelpout (*Lycodes palearis*), Pacific sandfish (*Trichodon trichodon*), and saddleback gunnel (*Pholis ornata).* Although not taxonomically related, these species were seldom represented by otoliths, individuals were very small, and with the exception of gunnels, were rare by number and frequency (Table 4). Little has been published about relationships between otolith length and fish length or fish length and mass for

Table 4

Average minimum number of individuals (MNI) per scat (total number of individuals identified in all scats collected in a season/total number of scats collected in a season) and frequency of occurrence (FO) for all skeletal remains and for otoliths exclusively for major prey taxa of harbor seals in the Columbia River during spring, summer, and fall. All = all skeletal remains.

	Spring				Summer				Fall			
	Average MNI/scat		FO		Average MNI/scat		FO		Average MNI/scat		FO	
Prey taxa	All	Otoliths	All	Otoliths	All	Otoliths	All	Otoliths	All	Otoliths	All	Otoliths
American shad	0.11	0.01	0.11	0.01	0.19	0.01	0.19	0.01	0.24	0.03	0.22	0.02
Cephalopod	0.01		0.01		0.02		0.02		0		0	
Elasmobranch	0.08		0.07		0.01		0.01		0.01		0.01	
Gunnel and prickelback	0.15	0	0.15	0	0.10	0	0.08	0	0.06	0	0.06	
Hexagrammid	0.02	0	0.02	0	0.01	0	0.01	0	0.03	0	0.03	
Lamprey species	0.35		0.26		0.35		0.25		0.08		0.06	
Northern anchovy	0.01	0	0.01	0	0.11	0.06	0.06	0.02	0.59	0.52	0.19	0.10
Other flatfish	0.41	0.25	0.20	0.07	0.16	0.03	0.12	0.03	0.28	0.12	0.18	0.06
Pacific hake	0.10	0.02	0.09	0.01	0.12	0.01	0.12	0.01	0.28	0.02	0.28	0.02
Pacific herring	0.53	0.24	0.36	0.09	0.88	0.52	0.57	0.21	0.29	0.16	0.22	0.09
Pacific mackerel	0.02	0	0.02	0	0	0	0	0	0.01	0	0.01	0
Pacific sand lance	0.12	0.06	0.10	0.04	0.03	0.01	0.03	0.01	0.02	0.02	0.02	0.01
Pacific staghorn sculpin	0.81	0.62	0.41	0.20	0.29	0.17	0.19	0.08	0.58	0.42	0.25	0.11
Pacific tomcod	0.21	0.09	0.18	0.06	0.13	0.05	0.09	0.02	0.51	0.24	0.39	0.13
Peamouth	0.04	0.02	0.03	0.01	0.11	0.06	0.08	0.03	0.08	0.05	0.05	0.02
Rockfish species	0.07	0.02	0.07	0.02	0.02	0.01	0.02	0	0.04	0.01	0.03	0.01
Salmon species—adult	0.07	0.04	0.06	0.03	0.06	0.04	0.04	0.02	0.10	0.02	0.10	0.01
Salmon species—juvenile	0.29	0.16	0.19	0.06	0.12	0.10	0.05	0.02	0.06	0.02	0.05	0.01
Shiner surfperch	0.08	0.04	0.07	0.02	0.23	0.15	0.18	0.05	0.14	0.10	0.08	0.04
Smelt species	0.42	0.31	0.28	0.12	0.35	0.30	0.18	0.11	1.27	1.21	0.35	0.21
Starry flounder	0.43	0.24	0.30	0.11	0.18	0.09	0.14	0.05	0.33	0.28	0.12	0.06
Unidentified flatfish	0.04	0.02	0.03	0	0.02	0	0.02	0	0.02	0	0.02	0

these families; rather than ignore their occurrence, these species were pooled and mass estimates were based on measurements of wattled eelpout and sandfish otoliths (Table 5). The family Scorpaenidae was composed mostly of juvenile fish (*Sebastes* and *Sebastelobus* spp.) which can seldom be distinguished to species from bones and otoliths. Mass estimates were based on black rockfish (*Sebastes melanops*; Table 5). Morphometeric relationships for peamouth (*Mylocheilus caurinus*) were unavailable in the literature. Peamouth are small, slender members of the minnow family, less than 36 cm in length, with a shape similar to several other small harbor seal prey. Mass was assumed to be less than 100 g. Hexagrammids included lingcod (*Ophiodon elongatus*) and greenlings (*Hexagrammos* spp.) also were poorly represented by otoliths. Mass was estimated from lingcod otoliths (Table 5). Because bones and otoliths were often difficult to identify to species, flatfish other than starry flounder were pooled and mass was calculated from the average of estimated masses of identified otoliths (rex sole, *Glyptocephalus zachirus*; English sole, *Pleuronectes vetulus*; Dover sole, *Microstomus pacificus*; rock sole, *Pleuronectes bilineatus*; slender sole, *Eopsetta exilis*) for each season. In contrast, starry flounder remains were easily identified and much more abundant than any other flatfish species (Table 4).

Several taxa were not represented by otoliths because they were completely digested or because the species lacked otoliths. No intact Pacific mackerel (*Scomber japonicus*) otoliths were recovered from scat and their mass was assumed to be less than 700 g, the upper limit reported by Eschmeyer and Herald (1983). Lamprey species included river (*Lampetra ayresii*) and Pacific lamprey (*L. tridentata*). Mass was estimated from the upper limit of outgoing Pacific and river lamprey from Pacific Northwest river systems (Beamish, 1980). Little information was available for predicting the mass of elasmobranchs; however, all elasmobranchs (spiny dogfish, *Squalus acanthias;* and skates, Rajidae) consumed by harbor seals appeared to be juveniles. Elasmobranch mass was extrapolated from a regression of vertebral centrum width on mass from another skate species (Zeiner and Wolf, 1993), yielding an upper estimate of 490 g. We assumed the mass of skates and spiny dogfish consumed by harbor seals to be of a similar size, and all less than 500 g. Cephalopod (*Loligo*

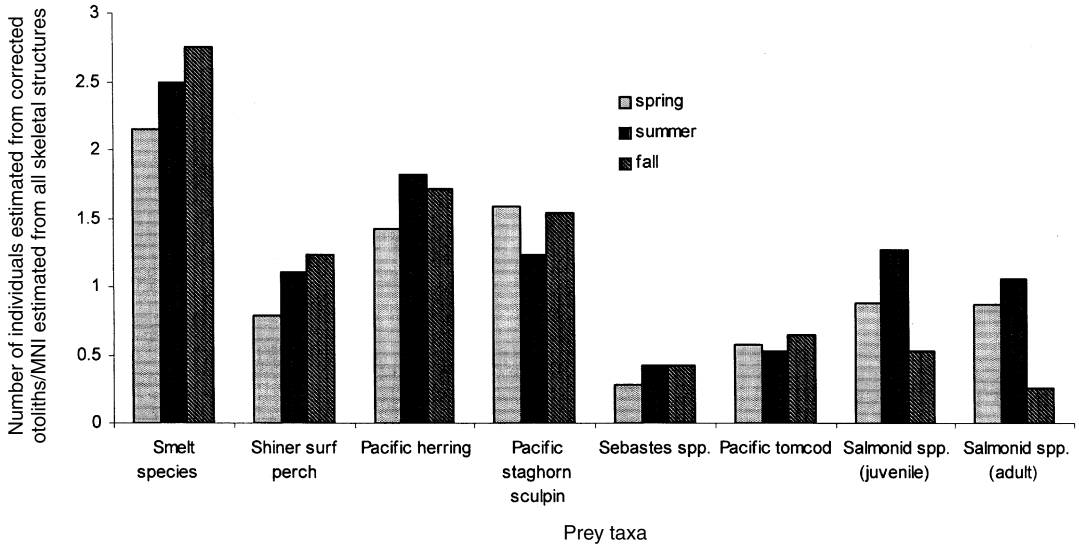

Figure 1

For eight prey taxa, ratio of estimated mean number of individuals estimated from the number of otoliths recovered from scat multiplied by a species-specific correction factor for recovery rate (Harvey, 1989) to MNI estimated from all structures recovered from harbor seal scats collected from Desdemona Sands during spring, summer, and fall 1995 through 1997. Values for smelt species are based on correction factors for eulachon. Values for salmonid species are based on correction factors for steelhead salmon.

opalescens and *Octopus* spp.) mass was estimated from regressions of beak measurements on mantle length and mass (Wolf, 1982).

Discussion

Diet of harbor seals in the Columbia River

Identification of prey remains indicated that the diet of harbor seals in the Columbia River was temporally variable and seals appeared to exploit prey when species were abundant. Many of the dominant prey by number and frequency were small fish such as herring, smelts, northern anchovy, juvenile flatfish, and sculpins (Tables 3 and 4). Pacific herring, Pacific staghorn sculpin (*Leptocottus armatus*), and smelts were three of the top six prey taxa by number and frequency for all three seasons (Table 4), although estimated masses varied greatly between season, indicating that seals preyed on different size classes (Table 5). Interestingly, scats without remains were most common during late spring and summer (Table 2). Olesiuk et al. (1990) reported similar results from British Columbia and suggested harbor seals were feeding on soft-bodied prey and roe. Occurrence of these scats in our study coincided with pupping on the lower Columbia River (Huber[6]), but an alternative explanation is that these may have been from nursing pups.

Most common harbor seal prey were variable by season or year (or both). Seasonal effects in the diet indicated periods when prey were reproducing, when young of the year were available, or perhaps an absence of highly abundant prey when seals relied more heavily on consistently available species. Annual differences in frequency of occurrence may have been largely the result of differences in sample timing or prey cohort strength (Moyle and Cech, 1982; Dark and Wilkins, 1994). Significant year and interactive effects between season and year probably reflected differences in prey year class (Table 3). For example, FO of anchovy (known to have high variability in recruitment) collected during fall of 1996 was 63%, whereas during fall of 1997 it was only 2%, although samples were collected on similar dates (Table 1). Harbor seals are generalist feeders and differences in frequency and number of prey probably reflect the temporal availability of prey rather than predator selection. This hypothesis is supported by AIC over-dispersion constants (b) greater than 1.0 for all prey taxa (Table 3). A binomial model assumes constant probabilities of a prey taxon occurring in scats collected on any sampling date within a season or year. Ephemerally abundant prey will have highly variable probabilities of occurrence in harbor seal scats collected in each season. It is likely that the overdispersion constant underestimates deviations for taxonomic groups, including more than one species such as salmonids and smelts, because temporal abundance of the different species in the group may be offset.

[6] Huber, H. R. 1997. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way, NE, Bldg. 4, Seattle, WA 98115.

Table 5

Average mass (g) of harbor seal prey, standard deviation (SD), and number of otoliths measured (n) for spring, summer, and fall prey of harbor seals in the Columbia River. Boldface values are estimates calculated from other seasons (when no intact otoliths were recovered within a season) or from literature sources (when no structures were available for measurement).

		Spring			Summer			Fall		
Family	Prey taxa	Avg. mass	SD	n	Avg. mass	SD	n	Avg. mass	SD	n
Clupeidae	American shad	198	22	4	517	601	5	523	284	11
	Pacific herring	93	35	50	96	64	238	97	73	54
Engraulidae	Northern anchovy	9		1	12	2	30	14	5	192
Osmeridae	Smelt species	15	23	84	6	2	147	7	3	331
Gadidae	Pacific tomcod	128	115	24	180	106	25	228	132	107
	Pacific hake	67		1	421		1	446	292	2
Pleuronectidae	Starry flounder	70	117	64	114	243	52	89	168	101
	Other flatfish	181	100	35	181	111	42	225	82	35
Cottidae	Pacific staghorn sculpin	140	84	136	160	84	88	115	42	45
Salmonidae	Chinook juvenile	206	150	22	41	93	21			0
	Chinook adult	1385		1	8515	6854	2	6862	1757	4
	Cutthroat juvenile	225	56	7	255	66	6	315		1
	Cutthroat adult	509	51	7	426	52	2			0
	Silver juvenile	277		1			0	88	103	2
	Silver adult	1607	983	2	671	241	15	4317	3545	3
	Steelhead juvenile	488		1	283	81	2			0
	Steelhead adult	1637		1	897		1			0
	Sockeye adult	2832		1			0			0
Embiotocidae	Shiner surfperch	79	39	7	85	43	80	79	42	45
Stichaeidae and Pholididae	Gunnels and prickelbacks	**90**	**84**	0	97	38	3	84	127	3
Hexagrammidae	Hexagrammids	**2090**	**1727**	0	3410	1375	2	756	135	2
Scorpaenidae	Rockfish species	187	87	6	132	7	2	114		1
Ammodytidae	Pacific sand lance	72	63	3	62	58	8	151		1
Elasmobranchs	Elasmobranchs	**500**		0	**500**		0	**500**		0
Scombridae	Pacific mackerel	**700**		0	**700**		0	**700**		0
Petromyzontidae	Lamprey species	**50**		0	**50**		0	**50**		0
Ptychocheilus	Peamouth chub	**100**		0	**100**		0	**100**		0
Cephalopods	Cephalopods	**21**	**1**	0	**21**	**1**	0			0

Salmon in the harbor seal diet

Harbor seals consumed several species and sizes of salmon throughout our study, but frequency was greatest during spring. Size of otoliths recovered indicated that most of these fish were juvenile chinook and that adult salmon were consumed to a lesser extent, primarily during fall. Fryer (1998) reported no difference in mean fork lengths of adult spring–summer *O. tshawytscha* with scars from pinnipeds and those without scars at the Bonneville Dam and observed a greater percentage of fish with scars earlier in the year, although these findings do not necessarily contradict data from our study. Scarred fish represent failed predation and perhaps harbor seals attempted to capture fish beyond their ability when spring run-off results in greater water turbidity. In addition, part of the discrepancy may be due to the classification of "adult" salmon. For our purposes, we categorized all fish with estimated lengths greater than outgoing migrants (30 to 35 cm depending on the species) as "adults." The mean lengths of scarred spring-summer *O. tshawytscha* from 1994 to 1996 (75.9 to 79.3 cm standard length) were greater than the mean length of "adult" fish estimated from prey remains (73.4 cm mean standard length).

Riemer and Brown (1997) also examined all skeletal structures; however, their results summarized data for four years and 154 samples collected on eight dates. Riemer and Brown (1997) reported salmon FO as great as 39% for a single sampling date but found no salmonid remains in scats collected during February and March.

Table 6

Harbor seal prey taxa ranked by minimum number of individuals (MNI) estimated from all skeletal structures and otoliths, frequency of occurrence (FO) estimated from all skeletal structures and from otoliths, and average mass of prey estimated from allometric relationships between otoliths and fish size. Prey are ranked for all seasons; i.e. smelt are the most numerically abundant prey over spring, summer, and fall. Data (as opposed to ranks) are presented in Tables 4 and 5.

Prey taxa	MNI all	MNI otoliths	FO all	FO otoliths	Mass
Smelt species	1	1	3	1	21
Pacific staghorn sculpin	2	2	1	2	10
Pacific herring	3	4	1	3	15
Starry flounder	4	6	5	5	16
Other flatfish	5	7	8	7	7
Lamprey species	5		5		19
Pacific tomcod	7	7	5	6	8
American shad	8	15	4	14	4
Shiner surfperch	9	7	10	8	18
Pacific hake	10	14	9	14	
Salmon species—juvenile	11	10	12	10	6
Northern anchovy	12	3	15	4	20
Gunnel and prickelback	13		11		17
Cephalopod	14		13		13
Pacific mackerel	15		14		3
Salmon species—adult	16	12	15	12	1
Peamouth	16	11	17	11	12
Pacific sand lance	18	13	18	13	14
Rockfish species	19	16	19	8	10
Unidentified flatfish	20	4	20		
Elasmobranch	21		21		5
Hexagrammid	22		22		2

Monthly FOs were based on a single sampling collection. During our study, FO of juvenile salmon was 50% on a sampling date during March of 1997; however, no salmon remains were found in scats collected a week earlier during 1995. Additionally, we found salmonid remains in harbor seal scat during every month of our data collection and we found no significant differences in the seasonal occurrence of adult salmonids. This finding, however, may have been due to our grouping species.

Harbor seals eat Columbia River salmon; however, they feed mostly on juvenile fish during the spring, and otolith identifications have indicated that most of these are chinook salmon. Currently, salmonid bone cannot be identified to species; however, the National Marine Mammal Laboratory is investigating identification of salmonid species from skeletal remains by using genetic techniques.

Comparison of identification methods

Identifying and enumerating prey from all skeletal structures is more time consuming than relying exclusively on otoliths and the described diet may be substantially different. MNI and FO both increase when all structures are used, particularly for taxa such as Pacific tomcod (*Microgadus proximus*), Pacific hake, American shad (*Alosa sapidissima*), salmon spp., hexagrammids, elasmobranchs, and lampreys that are vastly underestimated from otoliths or are entirely lacking in otoliths (Table 4). Relative importance of prey in the diet also may be dramatically affected (Table 6). Prey of the greatest estimated masses are ranked among the least important prey by number and frequency with the use of all skeletal elements and these prey are often completely absent from the diet described from otoliths. If one were to rely solely on otolith identifications, these prey could be entirely overlooked. The extrapolation of estimated biomass of each prey taxa from average mass estimated by otolith length and MNI estimated from all skeletal remains has a variety of caveats—namely, the relative contribution of large, infrequent prey may be vastly underestimated by using otoliths.

Although the identification of all structures increases the magnitude of both MNI and FO, estimates of the number of individual prey are likely to be less accurate. A description of pinniped diet from all prey remains is subject to many of the same biases inherent in otolith identifications. Identification of all skeletal structures assumes an equal probability of detecting all prey species and of recovering remains after consumption; these assumptions were violated to some extent in our study because, like otoliths, passage and identification of prey structures are taxon-specific (Harvey, 1989; Cottrell et al., 1996; Marcus et al., 1998). In captive experiments, herring (*Clupea pallasi*) were identified by 11 structures recovered in scats (other than otoliths), whereas smelt were represented only by vertebrae (Cottrell et al., 1996). Smelt vertebrae cannot be used to enumerate individuals, whereas several herring bones commonly recovered in scats are unique or are structures with definite sides (prootics, atlas and axis vertebrae), and even highly eroded herring bone retain characteristics identifiable to species. In contrast, bones of some taxa such as pleuronectids erode rapidly, losing species traits and are identified only to family. Given these factors, the identification of all skeletal structures represents the relative consumption of some prey more accurately than others. Further, MNI estimated from all skeletal structures is not corrected for complete digestion of structures useful for enumerating individuals. To date, there are no correction factors for complete digestion of bones and this lack, doubtlessly, is a source of substantial bias.

Behavior of both predator and prey also affects identification and enumeration of prey remains in scats. Small, schooling fish, such as smelts, are more likely to be consumed in greater numbers than larger, solitary fish such as hexagrammids. Smelts are most frequently identified from vertebrae; therefore MNI is more severely underestimated because more than one individual is likely to be consumed. Captive feeding studies also have indicated that the activity of the pinniped, its meal size, size of prey, and the physical structure of the prey bone all affect passage rate and the degree of erosion (Cottrell et al., 1996; Tollit et al., 1997; Marcus et al., 1998; Bowen, 2000).

The estimation of MNI from all prey structures recovered in scats presents a variety of complications; however, the alternative—using otolith correction factors—also has problems. Otolith correction factors based on recovery rates from feeding experiments are highly variable between repeated trials of the same individuals, different individuals, and different pinniped species (Harvey, 1989; Cottrell et al., 1996; Tollit et al., 1997; Bowen, 2000). Although his results were inconclusive, Bowen (2000) suggested that differences in activity levels may account for much of the variability in digestion (and correction factors). Activity levels among wild harbor seals are likely to be more variable than those between captive harbor seals with and without access to water, and thus otolith correction factors may yield erroneous estimates of individuals consumed by free-ranging predators. Limiting analyses of diet to qualitative measures such as FO will reduce the biases of including bone identification; however, the overall importance of frequent, small prey may be much less than indicated by their relative frequency.

Pinnipeds are considered generalist feeders and may feed on large numbers of abundant, frequently encountered prey; however, if mass is considered a measure of importance, they may be sustained by infrequent, large prey (Tables 4–6). A few prey species were both abundant and frequent (herring, smelts, sculpins, flatfish), yet their estimated masses were small. Large, infrequent species such as lingcod, hake, rockfish, and salmon may contribute more total mass to a hypothetical "meal." Unfortunately, these prey were also poorly represented by otoliths in our study and therefore our mass estimates may be inaccurate.

All methods of examining marine mammal diets, such as fecal analyses, stomach lavage, or stomach content analysis, are inherently biased to some degree. Biases of fecal analyses have been discussed at length in the literature; however, fecal analysis remains the least invasive and least expensive technique and allows for large sample sizes. Identification of all skeletal elements, rather than otoliths exclusively, is an improvement on other techniques. Although results are still subject to biases, prey taxa represented by hard parts in fecal material represent a minimum estimate of prey consumed. In addition, an examination of skeletal elements other than otoliths is mandatory for assessing the impact of harbor seals on certain prey species—protected salmon stocks, for example.

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