Examination of the foraging habits of Pacific harbor seal (*Phoca vitulina richardsi*) to describe their use of the Umpqua River, Oregon, and their predation on salmonids

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Abstract—The increase in harbor seal (*Phoca vitulina richardsi*) abundance, concurrent with the decrease in salmonid (*Oncorhynchus* spp.) and other fish stocks, raises concerns about the potential negative impact of seals on fish populations. Although harbor seals are found in rivers and estuaries, their presence is not necessarily indicative of exclusive or predominant feeding in these systems. We examined the diet of harbor seals in the Umpqua River, Oregon, during 1997 and 1998 to indirectly assess whether or not they were feeding in the river. Fish otoliths and other skeletal structures were recovered from 651 scats and used to identify seal prey. The use of all diagnostic prey structures, rather than just otoliths, increased our estimates of the number of taxa, the minimum number of individuals and percent frequency of occurrence (%FO) of prey consumed. The %FO indicated that the most common prey were pleuronectids, Pacific hake (*Merluccius productus*), Pacific staghorn sculpin (*Leptocottus armatus*), osmerids, and shiner surfperch (*Cymatogaster aggregata*). The majority (76%) of prey were fish that inhabit marine waters exclusively and fish found in marine and estuarine areas (e.g. anadromous spp.) which would indicate that seals forage predominantly at sea and use the estuary for resting and opportunistic feeding. Salmonid remains were encountered in 39 samples (6%); two samples contained identifiable otoliths, which were determined to be from chinook salmon (*O. tshawytscha*). Because of the complex salmonid composition in the Umpqua River, we used molecular genetic techniques on salmonid bones retrieved from scat to discern species that were rare from those that were abundant. Of the 37 scats with salmonid bones but no otoliths, bones were identified genetically as chinook or coho (*O. kisutch*) salmon, or steelhead trout (*O. mykiss*) in 90% of the samples.

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The Pacific harbor seal (*Phoca vitulina richardsi*) is found along the west coast of North America from the Aleutian Islands, Alaska, to the San Roque Islands, Baja California (King, 1983; Reeves et al., 1992). Before the passage of the Marine Mammal Protection Act (MMPA) of 1972, harbor seals in Oregon were kept at relatively low numbers (fewer than 500 animals in 1968) because of bounties offered by the state and harassment from commercial and sport fishermen (Pearson and Verts, 1970). Since passage of protective legislation, harbor seals in Oregon have increased an average of 6% to 7% annually between 1978 and 1998, although, in recent years, numbers appear to be leveling at about 8000 individuals (Brown and Kohlmann, 1998).

The rapid increase in harbor seal numbers has revived fishery-managers' interest in seal diet because of the potential for increased consumption of commercial fish species. In addition, there has been a heightened concern about greater harbor seal abundance in rivers and estuaries during migrations of depressed salmonid populations because of the potential negative impact on the recovery of these fishes (NMFS, 1997). Because of the tenuous status of many salmonid (*Oncorhynchus* spp.) species along the west coast, the National Marine Fisheries Service (NMFS) recommended that the United States Congress modify the MMPA to allow lethal removal of seals from river mouths where they may prey on depressed salmonid populations (NMFS, 1997). Predation of salmonids by harbor seals in Oregon has been documented (Brown, 1980; Harvey, 1987; Brown et al., 1995; Riemer and Brown, 1997; Beach et al.[1]). The proportion of salmonids in the diet of harbor seals varied from 1% to 30% depending on area, season, and sampling method (NMFS, 1997).

Pinniped prey consumption can be determined from direct observations in some systems, if prey is consumed at

[1] Beach, R., A. Geiger, S. Jefferies, S. Treacy, and B. 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. NWAFC 85-04, 316 p. NWAFC, National Marine Fisheries Service, Seattle, WA, 98115.

the surface (Bigg et al., 1990); however, consumption is typically determined by examining scat (fecal) samples. In the past, species-specific sagittal otoliths found in scats were used exclusively to determine the identification of prey taxa. However, because otoliths can be partially or completely digested, or are not present in scats (because the head of the prey was not consumed), they are not always an adequate representation of diet. Recently, investigators have begun to use additional structures (e.g. cranial elements, vertebrae) recovered from scats to identify prey (e.g. Olesiuk et al., 1990; Cottrell et al., 1996; Riemer and Brown, 1997; Browne et al., 2002; Lance et al.[2]). These structures usually are more common than otoliths and frequently can be identified to species; however, bones of some species can be identified to family only (e.g. salmonids). Consequently, the National Marine Mammal Laboratory (NMML) collaborated with the Conservation Biology Molecular Genetics Laboratory (CBMGL; Northwest Fisheries Science Center, Seattle, WA) to develop molecular genetic identification of salmonid species (Purcell et al., 2004). Because of the complex salmonid species composition in the Umpqua River, genetic identification was vital to distinguish species that were rare from those that were abundant.

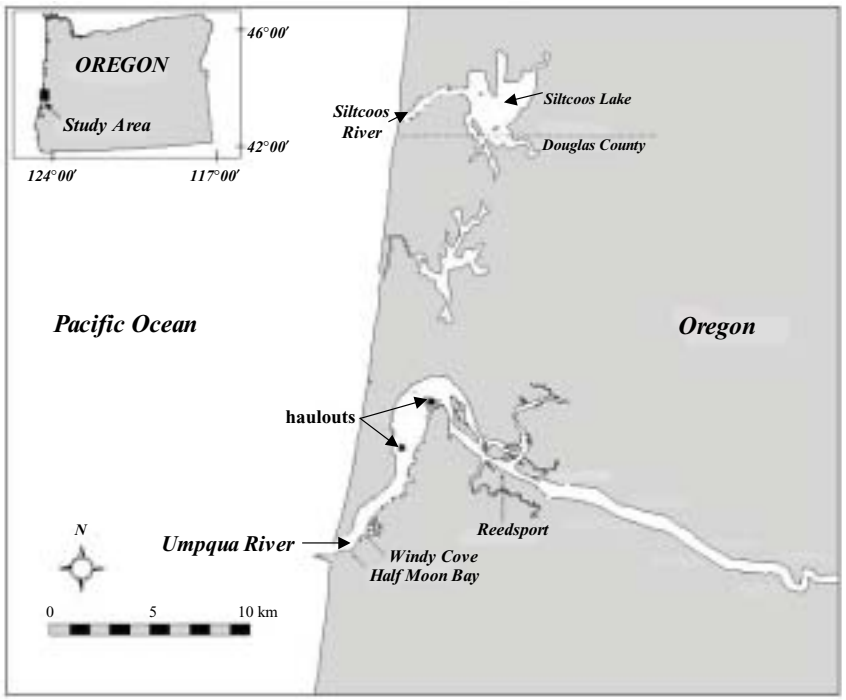

Figure 1

Map of the lower section of the Umpqua River, Oregon, where scat samples were collected at two haulout sites during 1997 and 1998.

The original impetus of this study was to assess the impact of harbor seal predation on the recovery of the Umpqua River sea-run cutthroat trout (*O. clarkii*) that were listed as endangered under the Endangered Species Act (ESA) during 1996 (Johnson et al., 1999). Umpqua River cutthroat trout were removed from the ESA in 2000 because they were identified to be part of the larger Oregon Coast evolutionary significant unit (U.S. Fish and Wildlife Service, 2000). The present study was continued despite the "delisting" of cutthroat trout because the Umpqua is inhabited year-round by harbor seals that haul out several kilometers upriver and is, thus, ideal for determining whether the presence of a pinniped species within a system is indicative of substantial feeding on fish species of concern within that environment. In addition, the Umpqua River contains several other salmonid species whose status is precarious (NMFS, 1997). Therefore, the development of genetic identification techniques was considered valuable for this system, as well as for future foraging studies in which species-specific identification may be desirable but impossible by way of conventional identification methods.

The objectives of this study were 1) to determine by an examination of diet if harbor seals that haul out in the Umpqua River feed primarily in the river or elsewhere, and 2) to apply genetic techniques to identify salmonid prey species.

Materials and methods

Study area

The Umpqua River, located in southern Oregon (Fig. 1), is a natal river for sea-run cutthroat trout, as well as chinook (*O. tshawytscha*), coho (*O. kisutch*) salmon, and steelhead trout (*O. mykiss*). The Umpqua estuary is also inhabited year-round by approximately 600–1000 harbor seals and has been designated as an area where pinnipeds and salmonids significantly co-occur (NMFS, 1997). Scat samples for this study were collected from two haulouts located within 4.8 km of the river's mouth and within 1.6 km of each other (Fig. 1).

Scat collection and analysis

Samples were collected during two seasons: "spring" (March through June) and "fall" (August to December). "Spring" corresponded to the migration of anadromous cutthroat trout adults and some juveniles to the ocean and "fall" coincided approximately with the freshwater return of spawning anadromous adults. The migratory and spawn-

[2] Lance, M., A. Orr, S. Riemer, M. Weise, and J. Laake. 2001. Pinniped food habits and prey identification techniques protocol. AFSC Proc. Rep. 2001-04, 36 p. AFSC, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

Table 1

Collection dates of harbor seal scats and numbers of scats with identifiable prey remains, without identifiable remains, and without remains from the Umpqua River, Oregon, during 1997 and 1998. Fall and spring periods correspond to timing of cutthroat trout runs on the Umpqua River.

Collection dates	With identifiable remains	Without identifiable remains	Without remains	Total
Fall, 1997				
16–23 Sep	26	1	2	29
27 Sep–6 Oct	5	0	3	8
12–24 Oct	31	0	7	38
31 Oct–10 Nov	21	0	6	27
12–25 Nov	36	0	10	46
Total	119	1	28	148
Spring 1998				
24–25 Mar	27	5	2	34
13–15 Apr	59	5	7	71
26–27 Apr	45	4	4	53
13–14 May	41	0	4	45
27–28 May	12	0	1	13
11–12 Jun	35	2	1	38
Total	219	16	19	254
Fall 1998				
5–6 Aug	142	1	1	144
19–20 Aug	111	1	3	115
6–9 Sep	28	3	3	34
19–21 Sep	13	0	0	13
7–8 Oct	19	0	1	20
Total	313	5	8	326

ing periods of chinook and coho salmon, and steelhead trout also occur during these times.

During fall 1997, all harbor seal scats present at the haulouts were collected every other day during the daytime low tide, weather permitting (Table 1). In 1998, biweekly attempts were made to pick a minimum of 50 scats during low tides at the haulout sites (Table 1). Scats were collected, placed in individual plastic bags, and frozen for later processing. At the laboratory samples were thawed and rinsed in nested sieves (1.0 mm, 0.71 mm, and 0.5 mm in 1997; 1.4 mm, 1.0 mm, and 0.5 mm in 1998). Fish structures were dried and stored in glass vials and cephalopod remains were stored in vials with 70% isopropyl or ethyl alcohol.

Prey were identified to the lowest possible taxon by using sagittal otoliths, skeletal, and cartilaginous remains from fish and beaks and statoliths from cephalopods. Other invertebrate remains were discarded from analysis because of the uncertainty of identifying them as primary or secondary prey. Unknown prey were categorized as "unidentified" and "unidentifiable" (Browne et al., 2002). Items that were categorized as "unidentifiable" were excluded from analyses because they could not be distinguished from prey already identified in the sample. Otoliths, beaks, and diagnostic bones were identified by using an extensive reference collection at the NMML and voucher samples verified by Pacific Identifications (Victoria, British Columbia).

After identification, otoliths were separated by side (left, right, or unknown) and enumerated to determine minimum number of specific prey. Unique diagnostic structures (e.g. quadrates, angulars, basioccipitals, vomers) were used for identification and enumeration of fish. Non-unique skeletal structures such as gillrakers and teeth were used to identify but not enumerate taxa (i.e. their presence indicated only a single individual) unless the structures were from different size classes. Vertebrae were treated like other non-unique structures; however, for salmon, if the number of vertebrae reflected more than one individual, then they were used for enumeration. Cephalopod beaks were separated by side (upper, lower, or unknown) and enumerated to determine number of prey.

To discern where harbor seals were feeding, identified prey were categorized as those exclusively found in rivers or estuaries (e.g. gobiids, cyprinids), those found exclusively in marine waters (e.g. gadids, myxinids), and those that could potentially be found in either environment (e.g. anadromous species, osmerids, petromyzontids) by using Eschmeyer et al. (1983). A seal was considered to feed in the river-estuary system if all the prey taxa identified in the scat were definitely or could potentially be found in the system. For example, a sample containing remains of pea-mouth chub (*Mylocheilus caurinus*), threespine stickleback (*Gasterosteus aculeatus*), river lamprey (*Lampetra ayresii*), and chinook salmon would be classified as a riverine-

estuarine species because these prey items could feasibly be consumed in the river. It was assumed that the seal was feeding in the marine environment if a sample contained exclusively marine prey, such as Pacific hagfish (*Eptatretus stoutti*), Pacific hake (*Merluccius productus*), and rockfish (*Sebastes* spp.). If a scat comprised prey taxa that potentially could be found in a riverine-estuarine system or marine waters (e.g. salmonids, osmerids), as well as those found exclusively in marine waters, then it was assumed that the feeding environment was marine or mixed.

Salmonid skeletal remains were sent to the CBMGL for species identification. Remains to be analyzed genetically were selected by number or size (or both) to represent different species or individuals present in each scat. For example, if a scat had 95 approximately equal-size vertebrae (a salmonid has approximately 65 vertebrae; Butler, 1990), then at least two vertebrae (potentially representing at least two individuals) were sent for genetic identification. Also, if a sample had a very large gillraker and three small vertebrae, then the gillraker and one vertebra were sent for genetic identification. The size of diagnostic structures was also used to categorize salmon remains as juvenile or adult, when possible. The CBMGL identified salmonid species by direct sequencing of mitochondrial DNA or analysis of restriction fragment length polymorphism (Purcell et al., 2004).

The abundance of prey taxa in harbor seal diet for each period was described by using the minimum number of individuals (MNI) and percent frequency of occurrence (%FO). We compared the effect of including bone on the number of prey consumed by estimating MNI using the greater number of right or left otoliths and then again using all diagnostic skeletal remains. Cephalopod MNI was estimated from the greater number of upper or lower beaks. The %FO of prey taxon *i* was defined as

$$\%FO_i = \frac{\sum_{k=1}^{s} O_{ik}}{s} \times 100,$$

where O_{ik} = absence (0) or presence (1) of taxon *i* in scat *k*; and

s = the total number of scats that contained identifiable prey remains.

The presence of taxon *i* in scat *k* was determined by using otoliths and then again using all structures. To account for variability in diet, point estimates of %FO for a prey taxon were determined during each sampling period and then averaged for each season.

Results

Scats

Over 725 scats were collected during all periods. The number of scats collected with identifiable remains was 119 (99%; *n*=148) in fall 1997, 219 (93%; *n*=254) in spring 1998, and 313 (98%; *n*=326) in fall 1998 (Table 1). Of the 651 samples with identifiable prey remains, 605 (93%) contained fish bones, 347 (53%) had fish otoliths, 231 (36%) contained remains from cartilaginous fish, and 41 (6%) had cephalopod beaks. A majority (65% fall 1997, 65% spring 1998, 63% fall 1998) of scats with identifiable remains had one to three prey taxa present and less than 4% contained more than ten taxa. Approximately 40 prey taxa, representing at least 25 families, were identified throughout the study (Tables 2 and 3).

For nearly all prey taxa, MNI was greater when all skeletal remains were identified than when otoliths were used exclusively (Table 2). For several species, such as Pacific hake, Pacific herring (*Clupea pallasii*), and Pacific sardine (*Sardinops sagax*), MNI at least tripled when all structures were used for enumeration (Table 2). For most salmonids, cartilaginous fishes, three-spine stickleback, Irish lords (*Hemilepidotus* spp.), and Pacific mackerel (*Scomber japonicus*), no otoliths were recovered; therefore other skeletal elements had to be used for identification (Table 2). For a few prey, such as cyprinids, gobiids, and butter sole (*Isopsetta isolepis*), only otoliths were recovered (Table 2).

Foraging habits

The %FO for most prey taxa was greater when all structures were used than when just otoliths were used (Table 3). The %FO indicated that the prey most frequently consumed were pleuronectids, Pacific hake, Pacific staghorn sculpin (*Leptocottus armatus*), osmerids, and shiner surfperch (*Cymatogaster aggregata*). Prey frequently found in scats included those that were exclusively marine (e.g. Pacific hake, rex sole (*Glyptocephalus zachirus*), English sole (*Parophrys vetulus*), and myxinids), and those that occur in both marine and estuarine waters (e.g. Pacific staghorn sculpin, and shiner surfperch [Table 3]). Only 24% of scats were composed entirely of prey taxa that could be found in riverine-estuarine systems (Fig. 2). Consequently, a majority of the scats contained prey species that were exclusively marine ($\bar{x}$=25.3%) or were a mixture of marine and potentially marine species ($\bar{x}$=50.8%; Fig. 2).

Salmonids

Salmonid remains were found in only 6% (39/651) of the samples. Five chinook smolts were identified from otoliths in two samples collected during fall 1997; in the remaining 37 samples, salmonid bones were unidentifiable to species with conventional techniques. With the cooperation of CBMGL, we examined 116 salmonid bones using molecular genetic techniques. Species identification was successful for 67% (78/116) of the bones and teeth from 90% (35/39) of the scat samples that contained salmonid structures. In the four samples that remained unidentified, three contained only a single salmonid bone that failed to produce any DNA. Most of the other bones where DNA could not be extracted were small or fragmented and highly digested. Seventeen of the samples contained chinook salmon bones (including the two samples with chinook salmon otoliths); 11 contained coho salmon bones, four contained steelhead trout bones, and three contained bones from two salmonid

Table 2

Minimum number of individuals (MNI) of fish prey derived from sagittal otoliths and all structures retrieved from harbor seal scats collected at the Umpqua River during 1997 and 1998. *s* represents the number of scats with identifiable remains. na indicates taxon did not have sagittal otoliths to be used for identification.

		Fall 1997 (*s*=119)		Spring 1998 (*s*=219)		Fall 1998 (*s*=313)	
Family	Species	MNI otoliths	MNI all structures	MNI otoliths	MNI all structures	MNI otoliths	MNI all structures
Ammodytidae	Pacific sand lance	205	208	317	321	3	7
Bothidae	Pacific sanddab	12	13	9	9	1	2
Clupeidae	American shad	1	2	4	11	1	15
	Pacific herring	6	22	3	10	121	345
	Pacific sardine	0	0	50	235	39	185
Cottidae	Pacific staghorn sculpin	44	65	25	48	30	85
	unidentified cottid	0	0	0	0	0	8
Cyprinidae	peamouth chub	1	1	4	4	4	4
Embiotocidae	shiner surfperch	104	109	209	274	23	104
Engraulididae	northern anchovy	1	3	0	0	1	2
Gadidae	Pacific hake	1	35	10	44	58	199
	Pacific tomcod	9	21	19	52	8	26
Gasterosteidae	threespine stickleback	0	1	0	0	0	0
Gobiidae	unidentified gobiid	2	2	1	1	0	0
Hexagrammidae	lingcod	0	1	0	0	1	1
Myxinidae	Pacific hagfish	0	20	0	13	0	61
Ophidiidae	spotted cusk-eel	0	0	4	4	2	2
Osmeridae	unidentified osmerid	42	54	14	41	105	132
Petromyzontidae	Pacific lamprey	na	5	na	89	na	41
	river lamprey	na	2	na	1	na	0
Pholididae	saddleback gunnel	3	7	1	3	0	1
Pleuronectidae	English sole	38	41	37	39	75	84
	Dover sole	1	4	5	6	27	51
	slender sole	1	1	18	24	28	42
	butter sole	1	1	15	15	2	2
	rex sole	19	44	44	53	96	125
	petrale sole	0	0	0	0	1	1
	starry flounder	10	17	8	12	6	31
Rajidae	unidentified rajid	na	1	na	7	na	4
Scombridae	Pacific mackerel	0	2	0	3	0	2
Scorpaenidae	*Sebastes* spp.	0	15	6	19	2	3
Trichodontidae	Pacific sandfish	0	0	0	1	2	3
Zoarcidae	unidentified zoarcid	0	0	0	0	2	2
Salmonidae	coho salmon						
	unknown	0	4	0	0	0	0
	juvenile	0	1	0	4	0	2
	adult	0	0	0	1	0	3
	Steelhead or rainbow trout						
	unknown	0	0	0	2	0	2
	juvenile	0	0	0	0	0	1
	chinook salmon						
	unknown	5	6	0	0	0	3
	juvenile	0	5	0	2	0	5
	adult	0	1	0	0	0	0
	unidentified salmonid						
	unknown	0	2	0	1	0	2
	juvenile	0	1	0	0	0	1

Table 3

Mean percent frequency of occurrence (%FO) of common prey recovered from harbor seal scat samples collected at haulout sites in the Umpqua River, Oregon, during 1997 and 1998. SD indicates standard deviation.

		Fall 1997	Spring 1997	Fall 1998
Family	Species	Mean (±SD)	Mean (±SD)	Mean (±SD)
Ammodytidae	Pacific sand lance	12.5 ±8.3	12.6 ±8.3	9.1 ±8.9
Bothidae	Pacific sanddab	11.4 ±7.5	4.1 ±2.5	3.0 ±3.2
Clupeidae	American shad	4.3 ±0.6	13.0 ±2.3	5.3 ±3.1
	Pacific herring	16.9 ±13.7	7.3 ±6.9	35.9 ±21.8
	Pacific sardine	0	16.1 ±12.2	17.9 ±9.1
Cottidae	Pacific staghorn sculpin	23.9 ±8.5	21.0 ±19.0	11.8 ±4.5
	unidentified cottid	16.5 ±20.4	3.2 ±0.7	0.8 ±0.1
Cyprinidae	peamouth chub	3.8	2.3 ±0.6	2.8
Embiotocidae	shiner surfperch	18.2 ±8.2	23.6 ±19.4	7.0 ±2.9
Engraulididae	northern anchovy	5.5 ±3.2	0	2.1 ±2.0
Gadidae	Pacific hake	27.9 ±9.7	17.0 ±5.7	41.6 ±25.5
	Pacific tomcod	15.4 ±7.8	16.1 ±7.0	12.3 ±8.3
Gasterosteidae	threespine stickleback	2.8	0	0
Gobiidae	unidentified gobiid	7.7	1.7	0
Hexagrammidae	lingcod	3.8	0	0.7
Loliginidae	market squid	12.8 ±10.2	3.5 ±1.3	0
Myxinidae	Pacific hagfish	17.5 ±7.9	6.7 ±3.5	16.5 ±9.4
Octopodidae	*Octopus rubescens*	3.8 ±1.4	8.3 ±2.6	8.4 ±7.0
Ophidiidae	spotted cusk-eel	0	0	0.9
Osmeridae	unidentified osmerid	20.8 ±11.3	14.6 ±8.2	19.5 ±10.0
Petromyzontidae	Pacific lamprey	7.7 ±8.2	20.5 ±10.1	8.2 ±2.9
	river lamprey	5.6	3.7	0
Pholididae	saddleback gunnel	14.7 ±16.9	2.6 ±0.3	5.3
Pleuronectidae	English sole	21.9 ±1.7	8.7 ±5.2	17.5 ±12.0
	Dover sole	7.4 ±5.9	4.6 ±0.7	13.5 ±13.6
	slender sole	0	11.0 ±7.2	14.9 ±14.9
	butter sole	3.8	7.2 ±3.7	1.4
	rex sole	27.4 ±12.1	14.2 ±9.6	19.9 ±20.5
	petrale sole	0	0	0.7
	starry flounder	15.8 ±7.4	3.7 ±1.0	5.8 ±1.2
Rajidae	unidentified rajid	2.8	5.0 ±1.6	2.8
Scombridae	Pacific mackerel	3.8 ±1.4	4.6 ±4.0	0.8 ±0.1
Scorpaenidae	*Sebastes* spp.	15.7 ±8.3	9.1 ±2.6	2.1
Trichodontidae	Pacific sandfish	0	1.7	2.1
unidentifed bothid/ pleuronectid	unidentified flatfish	38.5 ±15.9	20.2 ±10.3	14.8 ±2.5
Zoarcidae	unidentified zoarcid	0	0	1.4
Salmonidae	coho salmon			
	unknown	5.8 ±3.6	0	0
	juvenile	4.8	3.3 ±2.3	0.7
	adult	0	2.4	6.2 ±6.2
	steelhead/rainbow trout			
	unknown	0	2.7 ±1.4	0.7
	juvenile	0	0	0.9
	adult	0	0	0.9
	chinook salmon			
	unknown	7.6 ±3.5	0	0.8 ±0.1
	juvenile	4.0 ±1.1	3.4	3.6 ±3.0
	adult	4.8	0	0
	unidentified salmonid(s)			
	unknown	4.3 ±0.6	2.4	0.8 ±0.1
	juvenile	4.8	0	7.7

species (two with coho and chinook salmon and one with coho salmon and steelhead trout, Table 2). No cutthroat trout were identified with conventional or molecular genetic techniques.

Using otoliths and other diagnostic skeletal structures, we enumerated at least 54 individual salmonids in 39 scats (Table 2). All individuals identified as adults (n=5) were coho salmon, except one chinook salmon from spring 1997. Individual juveniles identified as steelhead trout (n=1), coho salmon (n=7), chinook salmon (n=12), or unidentified salmonids (n=2) were present during all periods. Because of the difficulty of determining age from size-variable structures such as gillrakers and teeth, most individuals (n=27) were designated as "unknown age."

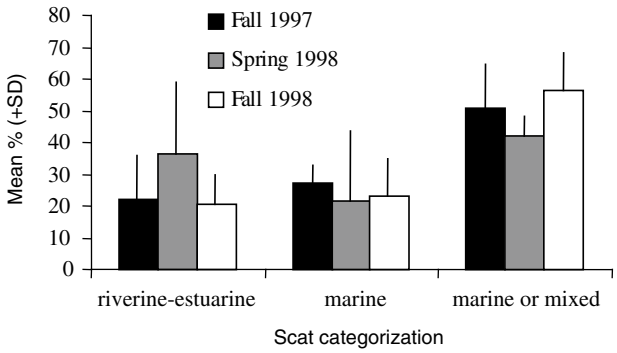

Figure 2

Mean percentage plus standard deviation (SD) of scats that were classified as "riverine-estuarine" (i.e. samples composed of prey taxa that are exclusively or potentially (e.g. anadromous species, osmerids) found in rivers or estuaries), "marine" (i.e. samples composed exclusively of prey that inhabit marine waters), and "marine or mixed" (i.e. samples composed of prey taxa exclusively found in marine waters or those that might inhabit marine waters at some stage in their life).

Discussion

Investigating diet is essential to assessing the role of harbor seals in marine and freshwater ecosystems in order to quantify their interactions with fisheries and determine their impact on the recovery of endangered species. All methods used to investigate diet of seals and other pinnipeds have some limitations (Murie and Lavigne, 1985, 1986; Harvey, 1989). With scats, it is assumed that the relative frequency of prey identified from undigested remains reflects the frequency of prey eaten (Tollit et al., 1997). However, several investigators have determined that this assumption may be seriously biased in several ways (Hawes, 1983; da Silva and Neilson, 1985; Jobling, 1987; Dellinger and Trillmich, 1988; Harvey, 1989; Pierce and Boyle, 1991; Cottrell et al., 1996; Tollit et al., 1997; Bowen, 2000; Orr and Harvey, 2001). No diet study can estimate detrimental or lethal impacts to prey resulting from harassment by pinnipeds. In addition, once a prey is captured, a seal might consume only the soft tissue (especially of larger prey), which would not leave identifiable evidence in scats. Additionally, because skeletal remains from different prey species pass through the alimentary canal and erode at different rates they may not reflect the true number or proportions of prey consumed (Hawes, 1983; Harvey, 1989; Pierce and Boyle, 1991; Cottrell et al., 1996; Tollit et al., 1997). Therefore, predation estimates determined from scat samples should be regarded as a measure of minimum impact. Although there are complications inherent in the use of scats to describe the diet of seals, scat analysis remains useful because many scats can be collected quickly, with minimum effort and without harm to the animals (Harvey, 1989).

Scats

Recently, skeletal remains other than otoliths and beaks have begun to be used to identify and enumerate prey of pinnipeds (e.g. Olesiuk et al., 1990; Cottrell et al., 1996; Riemer and Brown, 1997; Browne et al., 2002). There are constraints, however, for using all skeletal elements to identify prey species, including the need for a reference collection and the extensive training of personnel to identify digested prey structures (Cottrell et al., 1996). Moreover, there is usually a bias in the recovery and recognition of prey structures from different taxa (Cottrell et al., 1996; Laake et al., 2002). This bias may be a significant problem in estimating relative abundance of prey or biomass consumption by harbor seals and is the reason these indices were not considered in this study.

Despite these complications, the use of all available structures increased our estimates of prey diversity, MNI, and %FO for most prey taxa. Examination of all diagnostic structures also allowed us to consider a greater sample size because 93% of scats with identifiable remains contained bones, whereas only 53% of scats contained otoliths. Species not represented by otoliths, such as salmonids (during 1998) and cartilaginous fishes, were detected because all structures were used. In addition, the MNI of important prey such as Pacific hake, Pacific herring, and Pacific sardine would have been greatly underestimated had otoliths been used exclusively because the MNI derived by using all structures was at least threefold greater. Although there are complexities associated with estimating MNI from all structures, this method avoids the use of numerical correction factors determined from recovery rates of otoliths fed to captive seals during laboratory experiments (Browne et al., 2002). Results from captive experiments are highly variable between repeated trials for the same individual and among different individuals (Harvey, 1989; Bowen et al., 2000; Orr and Harvey, 2001).

Foraging habits

Harbor seals in the lower Umpqua River consumed prey from over 35 taxa; however, only a few prey taxa were dominant in their diet, as reflected by %FO. Overall, the five most abundant families of prey were Clupeidae, Cot-

tidae, Embiotocidae, Gadidae, and Pleuronectidae. These are similar to those reported in other studies of harbor seal diet in Oregon (Riemer and Brown, 1997; Browne et al., 2002; Riemer et al.[3, 4]).

It was evident by the presence of prey like Pacific hake, Pacific sardine, hagfish, and various flatfishes that seals fed offshore in pelagic and demersal areas. Harbor seals also consumed prey (e.g. Pacific staghorn sculpin) commonly found inshore or in estuarine waters. The NMFS recommendations to remove pinnipeds from systems where endangered prey also occur, rely on the assumption that pinnipeds are primarily feeding (on ESA-listed species) in that system. Our study indicated that this was not the case. Although the seals at the Umpqua hauled out several kilometers up river, they foraged primarily at sea.

Because of the life histories of many of the prey taxa, our foraging habitat categories must be considered estimations of where the prey might have been consumed. For example, we estimated that 24% of scats contained prey attributable to the riverine-estuarine environment. However, this may actually be an overestimation because some of these species potentially inhabit the marine environment at some time in their life and may have been consumed there. Additionally, scats categorized as marine or mixed may reflect that the seal fed solely in the marine environment (because all the taxa can potentially be found in marine waters) or fed at sea and within the river. Nevertheless, these categories are useful for a broad apportioning of foraging habitat. Even though we were able to determine that approximately 76% of the scats contained marine and potentially marine prey taxa, we were unable to assess whether this reflected a seal population with homogeneous or heterogeneous foraging patterns. In other words, because the scats could not be attributed to a particular individual, we had no way of discerning: 1) whether the entire seal population foraged roughly three-fourths of the time at sea and one-fourth of the time in the river, or 2) whether 76% of the seals fed at sea whereas 24% foraged closer to shore and in the river. This distinction may be important if only a subgroup of seals is feeding in the river and preying on fish that are seasonally abundant in the estuary, such as salmonids. Studies that incorporate radio- or satellite-telemetry or genetic identification of individual prey items in scats may reveal these distinctions in the future.

Because the seals haul out almost 5 km upriver and have been observed as far as 32 km upriver, it is clear that seals use the river environment. However, the prevalence of marine fish remains in the scat samples indicates that the seals that haul out at the Umpqua River do not feed exclusively in the river. The predominance of marine prey may reflect a foraging strategy in which the effort required to find marine sources of food is offset by the energy gained by exploiting large aggregations of marine schooling fish (e.g. Pacific hake and Pacific sardine). In this scenario, the seals in the Umpqua estuarine-riverine system may depend on marine resources while taking advantage of protected estuarine waters that provide a sheltered place to rest and occasionally feed.

Salmonids

We used two methods to estimate the number of salmonids eaten by harbor seals: prey remains and genetic analyses of scat samples. Analysis of skeletal remains was of limited value because the majority of salmonid structures recovered from scat samples were bones, which could be identified only to family. This study represents a novel application of genetic techniques to identify salmonid species from bones found in scats. These techniques allowed us to determine species for a majority of the salmonid samples that would have otherwise remained unidentified because they did not contain otoliths.

Salmonid bones or otoliths were found in 6% of the harbor seal scats collected during our study—a finding that is comparable to the 5% found by Laake et al. (2002) at the Columbia River. However, it is about one-half of what was found by Riemer and Brown (13%; 1997) at selected sites in Oregon. Brown et al. (1995) found salmonids in 12% of gastrointestinal tracts of harbors seals taken incidentally by commercial salmon gillnet fishing operations, and Roffe and Mate (1984) observed that salmonids made up 30% of the prey for harbor seals surface feeding in the Rogue River. Regardless of sampling method, in these studies, most of the salmonids could be identified only to family because few otoliths were recovered and genetic techniques to identify bones to species had not yet been developed.

Salmonids are present in the Umpqua River year-round although species and age composition change throughout the year. In this study, most salmonid prey of known age were juveniles; however, we could determine age of only one-half of the individuals. Juveniles are found in the Umpqua River system year-round and may be easier for seals to catch than adults. Alternatively, perhaps seals did not consume many adult skeletal elements because adult salmonids are large fish, which may be ripped apart rather than swallowed whole.

Our sampling seasons encompassed at least some portion of the migrations of all salmonids, all of which (except cutthroat trout) were prey of harbor seals. The fact that portions of all migrations were included in the sampling design was noteworthy because there were a large number of seals in the river throughout the year and yet we found no evidence through genetic or otolith identification that seals consumed cutthroat trout in the Umpqua River. The genetic identification tools developed and applied in our collaboration with CBMGL were useful in discerning

[3] Riemer, S. D., R. F. Brown, and M. I. Dhruv. 1999. Monitoring pinniped predation on salmonids in the Alsea and Rogue River estuaries: fall, 1997. *In* Pinniped predation on salmonids: preliminary reports on field investigations in Washington, Oregon, and California, p. 104–152. Compiled by National Marine Fisheries Service, Northwest Region. [Available from ODFW, 7118 NE Vandenberg Avenue, Corvallis, OR 97330.]

[4] Riemer, S. D., R. F. Brown, and M. I. Dhruv. 1999. Monitoring pinniped predation on salmonids in the Alsea and Rogue River estuaries: fall, 1998. *In* Pinniped predation on salmonids: preliminary reports on field investigations in Washington, Oregon, and California, p. 153–188. Compiled by National Marine Fisheries Service, Northwest Region. [Available from ODFW, 7118 NE Vandenberg Avenue, Corvallis, OR 97330.]

scarce from abundant salmonids. These techniques may be useful in identifying other pinniped prey that lack species-specific structures and would allow managers to better assess the impact of pinniped predation on threatened or endangered species.

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Literature cited

Bigg, M. A., G. Ellis, P. Cottrell, and L. Milette.
1990. Predation by harbour seals and sea lions on adult salmon in Comox Harbour and Cowichan Bay, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1769, 31 p.

Bowen, W. D.
2000. Reconstruction of pinnipeds diets: accounting for complete digestion of otoliths and cephalopod beaks. Can. J. Fish. Aquat. Sci. 57:898–905.

Brown, R. F.
1980. Abundance, movements and feeding habits of the harbor seal, *Phoca vitulina*, at Netarts Bay, Oregon. M.S. thesis, 69 p. Oregon State Univ., Corvallis, OR.

Brown, R. F., S. D. Riemer, and S. Jefferies.
1995. Food of pinnipeds collected during the Columbia River Area Commercial Salmon Gillnet Observation Program, 1991–1994. ODFW (Oregon Dep. Fish Wildlife), Wildlife Diverstiy Program Tech. Rep. 95-6-01, 16 p.

Brown, R. F., and S. Kohlmann.
1998. Trends in abundance and current status of the Pacific harbor seal (*Phoca vitulina richardsi*) in Oregon: 1977–1998. ODFW, Wildlife Diverstiy Program Tech. Rep. 98-6-01, 16 p.

Browne, P., J. L. Laake, and R. L. DeLong.
2002. Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples. Fish. Bull. 100:423–433.

Butler, U. L.
1990. Distinguishing natural from cultural salmonid deposits in Pacific Northwest North America. Ph.D. diss., 218 p. Univ. of Washington, Seattle, WA.

Cottrell, P. E., A. W. Trites, and E. H. Miller.
1996. Assessing the use of hard parts in faeces to identify harbour seal prey: results of captive-feeding trials. Can. J. Zool. 74:875–880.

da Silva, J., and J. Neilson.
1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Can. J. Fish. Aquat. Sci. 42:1439–1442.

Dellinger, T., and F. Trillmich.
1988. Estimating diet composition from scat analysis in otariid seals (Otariidae): is it reliable? Can. J. Zool. 66: 1865–1870.

Eschmeyer, W. N., E. S. Herald, and H. Hammann.
1983. A field guide to Pacific Coast fishes of North America, 336 p. Houghton Mifflin Co., Boston, MA.

Harvey, J. T.
1987. Population dynamics, annual food consumption, movements and dive behaviors of harbor seals, *Phoca vitulina richardsi*, in Oregon. Ph.D. diss., 177 p. Oregon State Univ., Corvallis, OR.
1989. Assessment of errors associated with harbor seal (*Phoca vitulina)* faecal sampling. J. Zool., Lond. 219: 101–111.

Hawes, S.
1983. An evaluation of California sea lion scat samples as indicators of prey importance. M.S. thesis, 50 p. San Francisco State Univ. San Francisco, CA.

Jobling, M.
1987. Marine mammal faeces samples as indicators of prey importance—a source of error in bioenergetics studies. Sarsia 72:255–260.

Johnson, O., M. Ruckelshaus, W. Grant, F. Waknitz, A. Garrett, G. Bryant, K. Neely, and J. Hard.
1999. Status review of coastal cutthroat trout from Washington, Oregon, and California. NOAA Tech. Memo. NMFS-NWFSC-37, 292 p.

King, J.
1983. Seals of the world, 240 p. Comstock Publishing Assoc., Cornell Univ. Press, New York, NY.

Laake, J. L., P. Browne, R. L. DeLong, and H. R. Huber.
2002. Pinniped diet composition: a comparison of estimation models. Fish. Bull. 100:434–447.

Murie, D., and D. Lavigne.
1985. A technique for the recovery of otoliths from stomach contents of piscivorous pinnipeds. J. Wildl. Manag. 49: 910-912.
1986. Interpretation of otoliths in stomach content analyses of phocid seals: Quantifying fish consumption. Can. J. Zool. 64:1152–1157.

NMFS (National Marine Fisheries Service).
1997. Investigation of scientific information on the impacts of California sea lions and Pacific harbor seals on salmonids and on the coastal ecosystem of Washington, Oregon, and California. NOAA Tech. Memo. NMFS-NWFSC-28, 172 p.

Olesiuk, P. F., M. A. Bigg, G. M. Ellis, S. J. Crockford, and R. J. Wigen.
1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. 1730, 135 p.

Orr, A. J., and J. T. Harvey.
2001. Quantifying errors associated with using fecal samples to determine the diet of the California sea lion (*Zalophus californianus*). Can. J. Zool. 79:1080–1087.

Pearson, J., and B. Verts.
1970. Abundance and distribution of harbor seals and northern sea lions in Oregon. Murrelet 51:1−5.
Pierce, G. J., and P. R. Boyle.
1991. A review of methods for diet analysis in piscivorous marine mammals. Ocean. Mar. Biol. Ann. Rev. 29:409−486.
Purcell, M, G. Mackey, E. LaHood, H. Huber, and L. Park.
2004. Molecular methods for the genetic identification of salmonid prey from Pacific harbor seal (*Phoca vitulina richardsi*) scat. Fish. Bull. 102:213–220.
Reeves, R., B. Stewart, and S. Leatherwood.
1992. The Sierra Club handbook of seals and sirenians, 359 p. Sierra Club Books, San Francisco, CA.
Riemer, S. D., and R. F. Brown.
1997. Prey of pinnipeds at selected sites in Oregon identified by scat (fecal) analysis, 1983–1996. ODFW Wildlife Diversity Program Tech. Rep. 97-6-02, 34 p.
Roffe, T., and B. Mate.
1984. Abundances and feeding habits of pinnipeds in the Rogue River, Oregon. J. Wildl. Manag. 48:1262−1274.
Tollit, D. J., M.J. Steward, P. M. Thompson, G. J. Pierce, M. B. Santos, and S. Hughes.
1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. Can. J. Fish. Aquat. Sci. 54:105−119.
U. S. Fish and Wildlife Service.
2000. Endangered and threatened wildlife and plants; final rule to remove the Umpqua River cutthroat trout from the list of endangered wildlife. Federal Register: 26 April 2000, 65(81:24420−24422.