Aquatic Mammals 2008, *34*(3), 303-309, DOI 10.1578/AM.34.3.2008.303

Resident Harbor Seals (*Phoca vitulina*) in Iliamna Lake, Alaska: Summer Diet and Partial Consumption of Adult Sockeye Salmon (*Oncorhynchus nerka*)

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Abstract

This study assessed the summer diet and consumption patterns of harbor seals (*Phoca vitulina*) resident in Iliamna Lake, Alaska. The authors predicted that adult sockeye salmon (*Oncorhynchus nerka*), a seasonally abundant and nutrient-rich prey source, would dominate diets when available and that seals would preferentially consume the most energetically profitable portion of salmon carcasses. Diet was examined by identifying hard parts of prey found in harbor seal scats, and consumption patterns were measured by collecting carcasses of harbor seal-killed sockeye salmon along island spawning grounds. Salmonids were present in 98% of scats that contained identifiable prey, followed by petromyzontids, osmerids, cottids, coregonids, and gasterosterids. The carcass surveys provided evidence of selective consumption patterns of sockeye salmon body parts. Harbor seals consumed the bodies of nearly all (96.6%) male salmon collected, leaving little but the head. In contrast, the belly and eggs were consumed in 63.6% of the female samples, and the entire body was eaten in only 31.3% of females. The harbor seals in Iliamna Lake thus took advantage of the seasonally abundant adult sockeye salmon by consuming them selectively and as a high proportion of their diet, but they also consumed smaller resident fishes, which presumably sustain them during the rest of the year.

Key Words: freshwater harbor seal, *Phoca vitulina*, sockeye salmon, *Oncorhynchus nerka*, Iliamna Lake, scat analysis, seasonal prey, selective predation, consumption patterns

Introduction

Harbor seals (*Phoca vitulina*) are among the most widely distributed pinnipeds, ranging throughout marine waters of the temperate and subarctic regions of the northern hemisphere (Bigg, 1981). Their diet varies among populations, locations, and seasons, reflecting both harbor seal behavior and the availability of prey (e.g., Harkonen, 1987; Payne & Selzer, 1989; Olesiuk, 1993; Iverson et al., 1997). Harbor seals are not strictly marine, and, in some areas, they commonly enter fresh waters adjacent to their marine habitats. Along the North American west coast, harbor seals temporarily enter rivers and estuaries where they forage on seasonally abundant anadromous fishes, particularly Pacific salmon (*Oncorhynchus* spp.) (Roffe & Mate, 1984; Stanley & Shaffer, 1995; Orr et al., 2004; Wright et al., 2007).

Despite this ability and tendency to forage in fresh water, harbor seals rarely establish year-round populations in freshwater environments. Seals in the Lacs des Loups Marins on the Ungava Peninsula of northern Québec and Iliamna Lake in southwest Alaska are the only freshwater populations recognized in the literature (Smith et al., 1996). Lacs des Loups harbor seals (*P. v. mellonae*) have received a subspecific classification based on morphological differences and isolation from other populations (Smith et al., 1994; Smith, 1997). They do not leave the lakes, and they forage exclusively on freshwater fishes (Smith et al., 1996). In contrast to the extensive work done on Lacs des Loups seals, studies of harbor seals in Iliamna Lake have been limited to aerial counts (Mathisen & Kline, 1992; Small, 2001), and no research has been done on their feeding ecology. The Iliamna Lake population is small, with maximum aerial counts of hauled-out harbor seals ranging from 137 (Mathisen & Kline, 1992) to 321 (Small, 2001). These counts do not indicate absolute abundance because these reports did not account for harbor seals that were in the water at the time counts were made. Iliamna Lake (approximately 121 km long and 32 km wide) is connected to Bristol Bay via the Kvichak River (approximately 80 km long). Although seals must

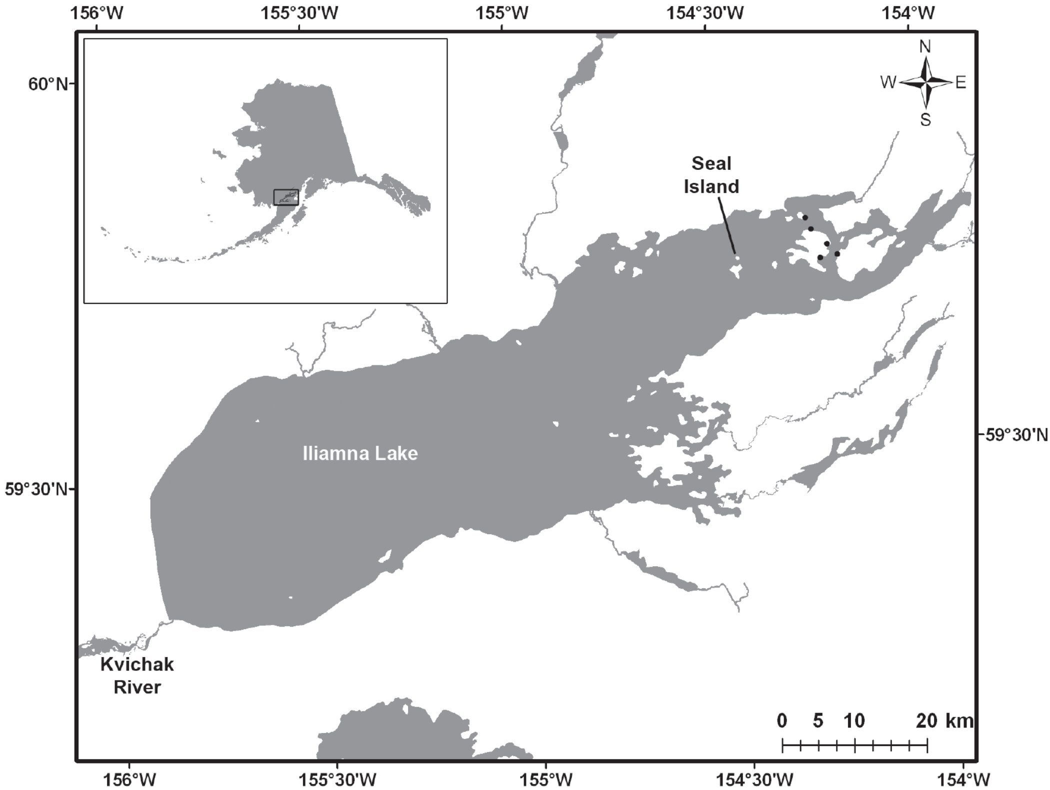

Figure 1. Map of Alaska showing detail of Iliamna Lake; black points indicate sockeye salmon beach spawning locations where carcasses were recovered.

have colonized Iliamna Lake from Bristol Bay via the Kvichak River (Figure 1), there is no evidence that regular movement up or down the river now occurs (Mathisen & Kline, 1992) nor are there any major impediments to movement. Primary haulouts are on islands located at the northeastern end of the lake, which is most distant from the outlet. Thus, current information indicates that these harbor seals are resident in the lake.

Iliamna Lake and its adjoining rivers contain several species of anadromous and resident salmonid fishes as well as petromyzontids (lampreys), cottids (sculpins), gasterosterids (sticklebacks), osmerids (smelts), and other fishes (Bond & Becker, 1963), which might be prey for seals (Table 1). In particular, the lake and its drainage system has supported the largest sockeye salmon (*Oncorhynchus nerka*) population of any lake in the world, with managers targeting annual post-fishery escapements of 2 to 10 million adults per year (Clark et al., 2006), although recent returns to the lake have been much lower. Adult sockeye enter the lake in late June and early July and remain there through mid to late August, after which most salmon have ascended streams to spawn or spawned in the lake itself. Juvenile sockeye emerge in spring and spend 1 or 2 y in the lake prior to seaward migration. They are potentially available year-round for consumption by harbor seals. Although it seems likely that Iliamna Lake harbor seals feed heavily or exclusively on adult salmon in the summer, there has been no study of this population's diet and the degree to which the salmonid resource is used.

Harbor seal diets are most frequently studied by examination of feces (e.g., Harkonen, 1987; Payne & Selzer, 1989; Olesiuk, 1993; Bowen & Harrison, 1996). Despite inherent biases in using scats to interpret seal diets (Pitcher, 1980a; Jobling & Breiby, 1986), diagnostic hard parts found in feces provide useful information and a dependable representation of the range of prey species consumed when multiple skeletal structures are used (Pitcher, 1980a; Harwood & Croxall, 1988; Browne et al., 2002). However, harbor seals sometimes only partially ingest large prey (Boyle, 1990; Tollit et al., 1997) and may selectively consume body parts. Such selective consumption reflects preferential foraging habits of harbor seals, and it also can be informative about possible biases in

Table 1. Family and species names of the fishes inhabiting the Kvichak River drainage (described in Bond & Becker, 1963) that are possible prey items for Iliamna Lake harbor seals

Family	Species
Petromyzontidae	Pacific lamprey (*Lampetra tridentatata*)
	Arctic lamprey (*Lampetra japonica*)
Salmonidae	Lake trout (*Salvelinus namaycush*)
	Arctic Char (*Salvelinus alpinus*)
	Dolly Varden (*Salvelinus malma*)
	Rainbow trout (*Oncorhynchus mykiss*)
	Pink salmon (*Oncorhynchus gorbuscha*)
	Coho salmon (*Oncorhynchus kisutch*)
	Chinook salmon (*Oncorhynchus tshawytscha*)
	Sockeye salmon (*Oncorhynchus nerka*)
	Chum salmon (*Oncorhynchus keta*)
Coregonidae	Round whitefish (*Prosopium cylindraceum*)
	Pygmy whitefish (*Prosopium coulteri*)
	Humpback whitefish (*Coregonus pidschian*)
	Least cisco (*Coregonus sardinella*)
	Arctic cisco (*Coregonus autumnalis*)
Osmeridae	Eulachon (*Thaleichthys pacificus*)
	Arctic smelt (*Osmerus eperlanus*)
	Pond smelt (*Hypomerus olidus*)
Gasterosteidae	Threespine stickleback (*Gasterosteus aculeatus*)
	Ninespine stickleback (*Pungitius pungitius*)
Catostomidae	Longnose sucker (*Catostomus catostomus*)
Gadidae	Burbot (*Lota lota*)
Cottidae	Slimy sculpin (*Cottus cognatus*)
	Coastrange sculpin (*Cottus aleuticus*)
Umbridae	Alaska blackfish (*Dallia pectoralis*)
Esocidae	Northern pike (*Esox lucius*)

using fecal samples as the basis for diet analysis. By way of comparison, examination of salmon carcasses has shown that brown and black bears (*Ursus arctos* and *U. americanus*) selectively consume salmon body parts to maximize energy density rather than biomass and that bears eat different body parts from males and females (Gende et al., 2001, 2004). Accordingly, the objectives of this study were to (1) use fecal samples to identify the primary prey items of harbor seals in Iliamna Lake during the summer when adult salmon were available and (2) describe harbor seal consumption of adult sockeye salmon by examining carcasses of harbor seal kills to determine the sex and patterns of body consumption.

Materials and Methods

Fecal samples were collected from a primary harbor seal haulout site in Iliamna Lake (Mathisen & Kline, 1992; Small, 2001), the spit of Seal Island (59.749° N, 154.442° W; Figure 1), during the peak of sockeye salmon spawning. Fresh scats were collected from 13 to 25 August 2001, 11 to 26 August 2005, and on 12 and 21 July 2006. Scats were placed in individual plastic bags and either processed within 24 h or frozen for later processing. Samples were rinsed through a series of sieves (mesh sizes 7.93, 6.68, 1.65, and 0.83 mm) to recover all hard prey remains.

Fish were identified by saggital otoliths and diagnostic skeletal elements to the lowest taxonomic level possible by comparison with reference specimens from the National Marine Mammal Laboratory in Seattle, Washington, and fish samples collected opportunistically at Iliamna Lake. Invertebrate remains were excluded from analysis because it was not possible to determine whether they were primary or secondary prey. Many samples did not contain otoliths and, therefore, identification often depended on more numerous skeletal structures such as vertebrae and teeth, which precluded enumeration of individuals. For most skeletal elements, identification to the species level was not possible, and prey were most commonly identified to the family level. We therefore used families as our unit for compiling and analyzing data. The prey group's relative importance was calculated as the percent frequency of occurrence (% FO)—that is, the percentage of all scat samples examined that contained a given prey. The number of prey groups per sample was used as a measure of prey diversity or group richness.

The eastern end of Iliamna Lake has many low-lying islands along which sockeye salmon spawn in August, in addition to the more typical spawning in tributaries. Spawning at these island beaches is concentrated in clear water less than a few meters deep, and the spawning areas can be readily surveyed by snorkeling (Quinn et al., 1996). Data on harbor seal-killed sockeye were collected during snorkel surveys on five beaches and adjacent reefs in August 2005, 2006, and 2007 (Figure 1). Salmon carcasses were examined, and those with bite marks were collected where possible or tallied if they could not be retrieved due to water depth. Carcasses with conspicuous bite marks and tissue loss were assumed to have been killed by harbor seals. Harbor seal bite marks appeared as a V-shape, which is different from the marks seen on bear-bitten salmon (see Gende et al., 2001). Bears are rare to absent on offshore islands, are unlikely to deposit carcasses in deeper water, and bear-killed salmon are typically found in shallow streams and riparian forests (Gende et al., 2001, 2004). The carcasses found in the lake were identified by sex (all were sockeye salmon), and consumption patterns were classified into three readily distinguishable categories: (1) *body* if the entire body was removed and only the head remained, (2) *belly* if only the ventral belly portion was consumed, and (3) *bite* if bite marks were present but no tissue was consumed. After examination, carcasses were discarded in deep water to avoid resampling.

Results

Fifty-one scat samples were collected from Seal Island (25 in 2001, 19 in 2005, and 7 in 2006), and 45 (88%) of them contained identifiable fish remains. The FO values among prey items did not differ between 2001 and 2005 ($\chi^2 = 6.82$, $p = 0.337$), so these data were pooled. Too few scat samples were collected in 2006 to be included in χ^2 comparisons with the other years, but similar patterns were observed, and these samples were pooled as well. Samples with identifiable items typically contained 1 to 3 (mean = 1.51, SD = 1.1) different families (59% of samples contained 1 family, 23% contained 2, 14% contained 3, 5% contained 4, and 2% contained 5). Prey items included at least six fish families, but only two could be identified to genus (*Lampetra* spp. and *Gasterosteus* spp.). Salmonids dominated the diet and were present in 98% of all samples containing identifiable prey (Table 2). Petromyzontids (27%) and osmerids (16%) were the next most common groups, followed by cottids (9%), coregonids (9%), and gasterosteids (7%).

Table 2. Name, sample size (*n*), and percent frequency of occurrence (% FO) of prey items from the 45 Iliamna Lake harbor seal fecal samples containing identifiable prey items

Prey item	*n*	% FO
Salmonidae	44	98
Petromyzontidae	12	27
Osmeridae	7	16
Cottidae	4	9
Coregonidae	4	9
Gasterosteidae	3	7
Unidentified	7	16

Table 3. Sample size (*n*) and percent frequency of occurrence (% FO) of salmonid structures of the 44 samples that contained salmonid remains

Salmonid prey item	*n*	% FO
Large vertebrae	37	84
Small vertebrae	13	30
Eggs	25	57
O. nerka otoliths	8	18
Large salmonid[1]	43	98

Note: Large vertebrae were typically ~10 mm in diameter, and small vertebrae were ~3 mm in diameter.
[1]Large salmonids were determined by the presence of either large vertebrae or eggs.

Of the 44 samples containing salmonid elements, two different size classes were present (Table 3). *Large* vertebrae (~10 mm diameter), most likely from adult *Oncorhynchus* spp. or large *Salvelinus* spp., were present in 84% of all salmonid samples. *Small* vertebrae (~3 mm diameter), most likely from juvenile or immature salmonids, occurred in 30% of all samples containing salmonid remains. Salmonid eggs were present in 57% of the samples containing salmonid hard structures. Otoliths from *Oncorhynchus* spp. were found in 18% of the samples with identifiable elements. Large salmonids were seen in at least 98% of the scats containing salmonid parts based on the presence of large vertebrae and/or eggs.

Nearly 1.1 million sockeye returned to Iliamna Lake in 2001, 2.3 million in 2005, and 3.1 million in 2006 (data available online from Alaska Department of Fish and Game: www.adfg.state.ak.us). At island spawning grounds and adjacent reefs, 157 adult sockeye salmon carcasses were sampled (58 males and 99 females). Ninety-six were sampled in 2005, 45 in 2006, and 16 in 2007. The distribution of consumption patterns for each gender of sockeye salmon did not differ among years (females, $\chi^2 = 5.03$, df = 4, $p = 0.284$; males, $\chi^2 = 0.66$, df = 4, $p = 0.956$), so these data among years were pooled. The body, posterior to the head, had been consumed in 96.6% of the males, leaving no tissue other than the head and sometimes the backbone (Table 4). Of the remaining male carcasses, 1.7% had the belly removed, and 1.7% only had bite marks with no tissue loss. In contrast, the belly had been consumed from 63.6% of the females, 31.3% had the entire body (other than the head) consumed, and 5.1% had bite marks but no consumption.

Table 4. Percentage consumption and sample sizes of male and female harbor seal-killed sockeye salmon carcasses; consumption by harbor seals was classified as full consumption of the salmon body (body), only removal of the belly portion (belly), or only a mortal bite without any flesh consumption (bite).

Year	Sex	% body	% belly	% bite	*n*
2005	Female	28.8	67.3	3.8	52
2006		39.5	52.6	7.9	38
2007		11.1	88.9	0.0	9
Combined		31.3	63.6	5.1	99
2005	Male	95.5	2.3	2.3	44
2006		100.0	0.0	0.0	7
2007		100.0	0.0	0.0	7
Combined		96.6	1.7	1.7	58

Discussion

Fecal samples from Seal Island indicated that harbor seals predominantly fed on adult salmonids during the summer period of high sockeye abundance. This finding corroborates previous evidence showing that other harbor seal populations feed on seasonally abundant prey (Brown & Mate, 1983; Payne & Selzer, 1989; Olesiuk, 1993; Iverson et al., 1997). However, adult salmon dominated the diets of Iliamna Lake harbor seals, whereas in marine environments, salmonids typically contribute less than 10% of a diet estimated on the basis of scats (e.g., Olesiuk, 1993; Orr et al., 2004; Wright et al., 2007). Large salmonid parts (bones, otoliths, or eggs) were found in almost all scat samples, whereas small salmonids were evident in < 30% of samples. The large salmonids were most likely adult sockeye salmon. The lake also supports populations of lake trout (*S. namaycush*) and Arctic char (*S. alpinus*) that are primarily lake residents, and rainbow trout (*O. mykiss*) and Dolly Varden (*S. malma*) that often migrate between rivers and the lake. Had these species been the primary prey during our sampling period, a greater number of smaller vertebrae would be expected than was observed. There are no quantitative estimates of the abundance of these fish in the lake itself, but summer observations indicate that sockeye salmon dominate the large-bodied fish community in the littoral zone. Sampling of small-bodied fishes found in the limnetic zone reveals that juvenile sockeye salmon and threespine sticklebacks are numerically dominant while other species are quite rare (Rich, 2006). Adult sockeye salmon enter the lake in late June and early July, and most have either departed the lake for riverine spawning habitats or spawned on lake beaches and died by late August through early October. Thus, for 2 to 3 mo, there are large numbers (typically millions) of adult sockeye, but for the rest of the year, there are only juveniles and the other resident fishes for the seals to eat.

Although adult salmonids occurred with the highest frequency in samples, the harbor seals also ate smaller or juvenile salmonids as well as lamprey and smelt, and occasionally whitefish, sculpins, and sticklebacks. This is likely more representative of the diet during the rest of the year when adult salmon are absent. It is possible that harbor seals may attack and ingest salmon with parasitic lamprey attached; however, it is thought that both Pacific and Arctic lampreys (*L. tridentatata* and *L. japonica*, respectively) are only parasitic during ocean life stages (Heard, 1966; McPhail & Lindsey, 1970; Scott & Crossman, 1973), and the authors have not observed adult sockeye in the lake with lamprey attached. Thus, the presence of lamprey in harbor seal diets likely represents primary consumption. Sticklebacks were present in scats from 2001 (13% FO) but were absent from the 2005 and 2006 samples. *Schistocephalus solidus* (a parasitic worm common in three-spine sticklebacks) was present in 21% of the 2005 samples, however, indicating that the harbor seals may in fact have been feeding on sticklebacks. The presence of *Schistocephalus* was not determined in 2001. If it was incidental to stickleback consumption, stickleback occurrence would be greater than indicated by the presence of bony parts (17% FO with *Schistocephalus*, 6% FO without *Schistocephalus*).

The carcass survey provided an independent source of information on Iliamna Lake harbor seal predation to compare with scat samples. Seal Island is about 2 km away from the nearest sockeye spawning areas and 10 to 30 km from larger concentrations of spawning adult salmon, but it is common to see harbor seals near beaches where sockeye salmon spawn. Spawning behavior in shallow water may make salmon more vulnerable at these islands than in open water, but there is no way to assess consumption patterns elsewhere in the lake. At these spawning beaches, we are confident that carcasses of partially consumed sockeye were killed by harbor seals and not bears because they were under water, away from shore, had different bite patterns than are typically caused by bears (see Gende et al., 2001), and were at locations where bears are seldom present. Distinctive patterns of bear predation such as consumption of the brain of both sexes and dorsal hump, especially from males (Gende et al., 2001), were not seen on the recovered carcasses, further indicating that bears were not responsible for the mortality. None of the carcasses retrieved were missing all or part of the head, but 18% of the scat samples with salmonids contained otoliths. It is possible that some sockeye were fully consumed, leaving no carcass to be sampled. Other studies similarly suggested that harbor seals do not commonly eat the heads of large prey such as adult salmonids (Pitcher, 1980b; Roffe & Mate, 1984), although Brown & Mate (1983) occasionally observed harbor seals eating chum salmon (*O. keta*) heads during surface observations in Netarts Bay, Oregon. Furthermore, otoliths from salmonids are more fragile than other bones and are not commonly recovered in pinniped scats (London, 2006), which reinforces the importance of using multiple skeletal structures to identify prey (Browne et al., 2002).

The presence of eggs in fecal samples and the frequent consumption of bellies only from female salmon indicated that harbor seals selectively consumed energy-rich parts of pre-spawning females. In most cases, when males were killed, the entire body was consumed, consistent with the lack of especially energy-rich body parts in males. The brains of salmon are rich in energy, though small in volume (Gende et al., 2004), and they are preferentially consumed by bears, especially those feeding on male salmon (Gende et al., 2001). The sockeye salmon are semelparous and invariably die at the end of the spawning season, presenting harbor seals with a vast supply of biomass. However, dead fish are much lower in energy than pre-spawning salmon (Gende et al., 2004).

This work is the first to document prey use of harbor seals in Iliamna Lake, and it indicates a strong reliance on adult sockeye salmon during July and August. It is still unclear what the presumably resident harbor seals eat when adult sockeye salmon are not available. It is likely that there is a greater dependence on resident fishes and perhaps sockeye smolt during other times of the year based on the fact that even summer samples contained small fishes from diverse taxa. Adult sockeye may play an important role in supporting this harbor seal population, however, by providing a rich seasonal food supply, just as salmon play an important role in the population biology of many other animals (e.g., Hilderbrand et al., 1999).

Acknowledgments

We thank all of the Alaska Salmon Program staff and AERA students who contributed to this project, particularly Keith Denton and Greg Buck. This manuscript has been greatly improved by insightful reviews by John Burns and Lloyd Lowry. Tony Orr, Glenn VanBlaricom, and Peter Westley offered additional editorial comments. Funding was provided by the School of Aquatic and Fishery Sciences at the University of Washington, National Science Foundation's BioComplexity Program, and the Gordon and Betty Moore Foundation.

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