Application of two methods for determining diet of northern fur seals (*Callorhinus ursinus*)

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Abstract—Examination of hard parts recovered from scats (feces) is currently the most common method for determining the diet of pinnipeds. However, large or sharp prey remains may be spewed (regurgitated) biasing prey composition and size estimations in diet studies based on scats. Percent frequency of occurrence (FO%) and age or size of selected prey remains recovered from northern fur seal (*Callorhinus ursinus*) scat (*n*=3444) and spew samples (*n*=267) collected from rookeries on St. George Island and St. Paul Island, Alaska, between 1990 and 2000 were compared to determine if a bias in prey composition and age or size estimations existed between scats and spews.

Overall prey composition was similar between sample type and location, but the relative FO% of primary prey (≥5%) varied by sample type and location. Age or size estimates of walleye pollock (*Theragra chalcogramma*) and of two species of gonatid squids (*Gonatopsis borealis* and *Berryteuthis magister*) were significantly larger in spews than in scats. Observed differences in FO% and estimated age or size of prey species whose remains were found in scats and spews likely result from size-selective digestion of prey remains. Scats were biased toward smaller prey remains, whereas spews were biased toward larger prey remains and cephalopod beaks. The percent overlap between age classes of walleye pollock caught by the commercial trawl fishery and age classes of walleye pollock consumed by northern fur seals varied noticeably between sample types for both islands (scats: St. George=15. 5%; St. Paul=4.1%; spews: St. George=94.6%; St. Paul=89.6%). These results demonstrate that the inclusion of multiple sampling methods allows for a more accurate assessment of northern fur seal prey occurrence and prey age and size.

Pinniped diet analysis involves the identification of prey remains recovered from a variety of sample types. Prey remains are obtained from stomach lavage and enema procedures from feces (scats) and regurgitations (spews), and from stomachs and gastrointestinal tracts. Historically, northern fur seal (*Callorhinus ursinus*) diet studies have relied upon analysis of stomach and intestinal contents collected from scientific takes or harvested animals (Wilke and Kenyon, 1957; Kajimura, 1984; Bigg and Fawcett, 1985; Sinclair et al., 1994) and, more recently, scat samples (Sinclair et al., 1996; Antonelis et al., 1997). Because a thorough analysis of gastrointestinal contents generally requires the sacrifice of an animal, intact gastrointestinal specimens are no longer typically used in diet analyses. Lavage and enema procedures are also not widely used to describe the diet of the population because sample sizes are often small and animals may require chemical immobilization, thereby increasing the risk of injury or fatality (Antonelis et al., 1987; Harvey and Antonelis, 1994).

Presently, scats are the most commonly used sample type in pinniped diet analyses because they are easy to collect, abundant, and noninvasive (Harvey, 1989; Hammond and Prime, 1990). However, many studies have demonstrated the potential biases associated with this sampling method (Jobling and Breiby, 1986; Pierce and Boyle, 1991; Bowen, 2000), including the accumulation of cephalopod beaks

in the stomach (Bigg and Fawcett, 1985; Gales et al., 1993; Harvey and Antonelis, 1994) and underestimation of size and frequency of occurrence of some prey species (Bigg and Fawcett, 1985; Harvey, 1989; Tollit et al., 1997). Captive feeding studies of numerous pinniped species have shown that factors such as species, sex, individual activity level, stomach size, gut length, prey digestibility, feeding regime, and meal size affect the degree of erosion and recovery of prey remains in scats (Harvey and Antonelis, 1994; Tollit et al., 1997; Marcus et al., 1998; Bowen, 2000; Orr and Harvey, 2001). Although studies have been conducted to account for these biases through the use of correction factors (Sinclair et al., 1994; Antonelis et al., 1997; Tollit et al., 1997), the different retention and digestive rates of prey remains in the stomach continue to be a leading criticism for diet studies in which scat samples alone are used.

Spews have been analyzed for several species of pinnipeds (Gales et al., 1993; Harvey and Antonelis, 1994; Kiyota et al., 1999; Lowry and Carretta, 1999; Kirkman et al., 2000). Spews contain prey remains such as fish bones, otoliths, and cephalopod beaks. Often these prey remains are too large to pass through the pyloric sphincter and are, therefore, regurgitated from the stomach (Bigg and Fawcett, 1985; Jobling and Breiby, 1986). Although spewings may be found in areas where pinnipeds come ashore, they are often less abundant

than scats (Jobling and Breiby, 1986; Gales et al., 1993) and have largely been excluded from pinniped diet analyses. Spews from northern fur seals are present on summer breeding islands, but diet studies that are based on spews are limited (Kiyota et al., 1999).

Our study is a comparative evaluation of diet based on scat and spew samples collected from northern fur seal breeding rookeries on two islands in the eastern Bering Sea. Prey remains in scat and spew samples were compared for prey species composition, and the age or size of walleye pollock (*Theragra chalcogramma*) and of two species of gonatid squids (*Gonatopsis borealis* and *Berryteuthis magister)* were estimated. Finally, we compared age classes of walleye pollock found in scats and spewings to age classes of walleye pollock caught by the commercial trawl fishery in management regions adjacent to the Pribilof Islands.
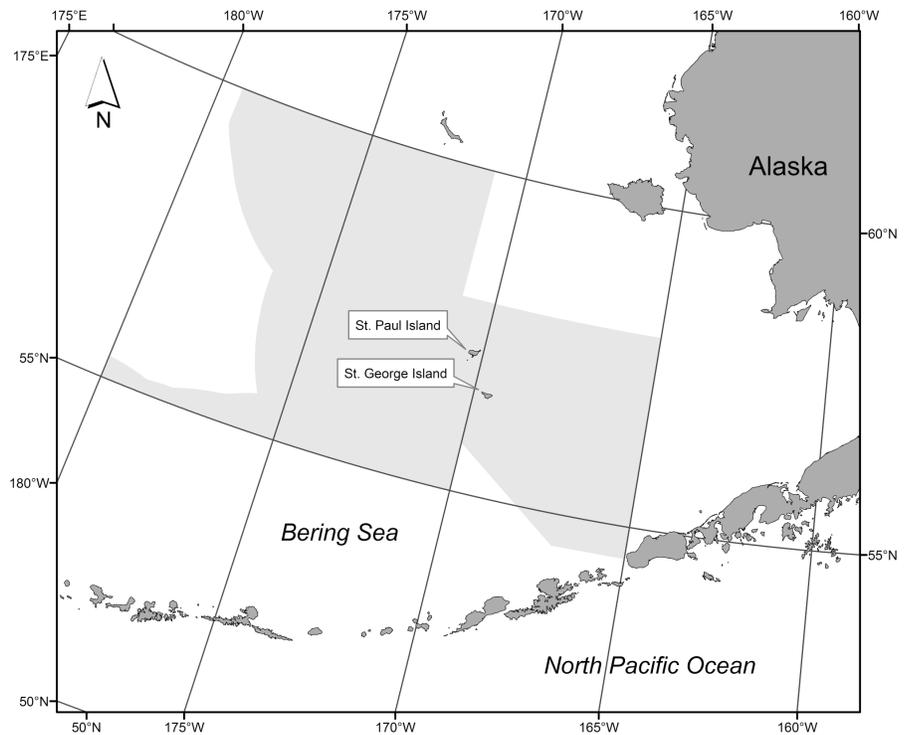
Figure 1

Location of St. George Island and St. Paul Island, within the Pribilof Islands, Alaska. Shaded area indicates walleye pollock (*Theragra chalcogramma*) commercial trawl fishery management areas surrounding the Phibilof Islands.

Materials and methods

Sample collection and processing

Scats and spews were collected opportunistically from rookeries on the Pribilof Islands (St. George and St. Paul), Alaska (Fig. 1), during the breeding season between 1990 and 2000. Samples collected from rookeries during this time (late July through September) were considered to be primarily from females of breeding age (Antonelis et al., 1997). Each scat and spew sample was placed in a plastic bag and frozen until it was analyzed in the laboratory. Samples were thawed and soaked in a mild emulsifying soap solution then rinsed through nested sieves of 4.75, 1.4, 1.0, and 0.5-mm mesh. Bones, otoliths, beaks, and eye lenses were recovered from the sieved samples and stored for analysis. Bones, otoliths, and eye lenses were stored dry in vials and beaks were stored in vials containing 50% isopropyl alcohol (Antonelis et al., 1997). Recovered diagnostic fish bones, otoliths, and cephalopod beaks were identified to the lowest possible taxon by comparing them to a reference collection. Distinctions, based on the morphological features of beaks, between some cephalopod species within the family Gonatidae were not possible. Therefore, identifications of four squid species known to occur in northern fur seal diet were categorized into two groups following Sinclair et al. (1994) and Antonelis et al. (1997) and are referred to as Gb-Bm (*Gonatopsis*

borealis and Berryteuthis magister) and Gm-Gm (*G. madokai* and *G. middendorfii*). Additionally, distinctions between four gonatid species (*Eogonatus tinro*, *G. berryi*, *G. pyros*, and *G. onyx*), were difficult to determine from the morphological features of beak and, collectively, are referred to as "gonatid group I" in the present study.

Prey indices

Individual prey species and prey groups were analyzed according to their frequency of occurrence (FO) in scats and spews for both islands. The percent frequency of occurrence (FO%) was calculated by dividing the number of scats or spews containing a specific prey species or group by the total number of scats or spews containing identifiable prey remains. Data from each year were pooled for FO% calculations because of low sample sizes in some years. Prey species or groups with a FO% ≥5% when rounded to the nearest integer, for either island or sample type, were considered to be primary prey.

The minimum number of individuals (MNI) of each prey type was calculated for each sample, and summed over all samples. The cephalopod MNI was estimated by using the maximum count of either upper or lower beaks in each sample. Fish MNI was estimated by using the maximum count in each sample from left or right otoliths, plus half of the otoliths for which a side (right or left) could not be determined (Antonelis et al., 1997). Percent MNI (MNI%) was then calculated by

dividing the MNI of each prey species or group (for all samples) by the total MNI of all prey for samples that contained identifiable fish otoliths or cephalopod beaks (or both).

To determine if the occurrence of prey varied by island or sample type (or both), the presence or absence of the primary prey (n=number of scats with prey remains) was modeled as a binomial random variable by using generalized linear models with island, sample type, and the interaction of island and sample type as explanatory variables (S-PLUS 2000, Insightful Corp., Seattle, WA). The interaction was considered significant if adding the interaction significantly reduced the deviance in the model. If the interaction was significant, islands within each sample type or sample types within each island were compared, depending on whether sample type or island reduced more of the overall deviance. If the interaction was not significant, it was removed from the model, and island and sample type effects were tested. Even though data were insufficient to test for differences in prey occurrence between years, year was included in the model as an additive variable.

Comparisons of prey age and size

Recovered walleye pollock otoliths were assigned a condition grade ("good," "fair," or "poor") based on distinctive features such as sulcus definition, shape, chipping, breaks, and wear (Sinclair, 1988). Pollock otoliths of "good" or "fair" condition were measured lengthwise parallel to the sulcus to the nearest 0.1 mm using hand-held digital calipers. A correction factor was applied to "fair" otoliths to account for loss of otolith length as a result of digestion (Sinclair, 1988; Antonelis et al., 1997). Fork lengths of prey were estimated by using regression formulae of otolith length against body length (Frost and Lowry, 1981) and age class was estimated from fork-length–age relationships (Sinclair et al., 1994). Pollock otoliths of "poor" condition were enumerated, but not measured, and were not included in prey size comparisons because of their high degree of erosion.

Pollock otoliths recovered from scat samples processed in the early 1990s were measured, but only age class estimations were recorded in the database. Therefore, to test how the size of walleye pollock otoliths varied by sample type and island, otoliths of "good" and "fair" grades were combined into two age categories; juvenile (0–2 age) and adult (3–5+ age) and each sample (scat or spew) was categorized as containing juvenile, adult, or mixed (juvenile and adult) pollock. Multidimensional contingency tables with island, sample type, and age category as variables were used to test interactive effects among variables. A saturated model including all variables and interactions was compared with restricted models by using chi-square goodness-of-fit test (S-PLUS 2000, Insightful Corp., Seattle, WA). Samples were pooled if sample type or island effects were conditionally independent, and two-dimensional contingency tables were then used to test variables that were not independent.

The size range of Gb-Bm consumed by northern fur seals was estimated by measuring the rostral length of lower beaks recovered from scat and spews. Rostral length was measured to the nearest 0.1 mm with an optical micrometer. Because cephalopod beaks are more resistant to digestion and to subsequent loss of length than are otoliths (Sinclair et al., 1996; Tollit et al., 1997), Gb-Bm lower beaks were not assigned condition grades prior to being measured. However, lower beaks showing excessive wear, such as a broken rostral tip, were not measured.

To evaluate Gb-Bm prey size differences between sample type and islands, we developed (using combined samples of both species) regression equations for lower beak rostral length (LRL) against dorsal mantle length (DML) and for DML against weight. Squid specimens were opportunistically collected from commercial pollock trawl fishery bycatch, research driftnets, and NOAA research vessel mid-water trawl operations between 1979 and 2000. Sampling areas were broad ranging throughout the North Pacific, at numerous localities in the eastern Bering Sea, Gulf of Alaska, and subarctic Pacific Ocean south of the western Aleutian Islands (Walker[1]).

The regression of LRL against DML for Gb-Bm was developed by using 757 lower beaks (n=482 Gb, 275 Bm) with a dorsal mantle length range of 21–386 mm and the DML-weight regression was developed by using 1676 lower beaks (n=1048 Gb, 628 Bm) with a dorsal mantle length range of 17–386 mm. The regression included size ranges of Gb-Bm found in northern fur seal scats and spews examined in the present study. Linear models were used to develop regressions of LRL (mm) against DML (mm) and DML against weight (grams):

$$DML = 39.3 \ (LRL) - 0.5 \ .$$
$$\mathrm{Lo} \ (weight) = 2.87 \big(\mathrm{Lo} \ (DML)\big) - 4.1 \ .$$

A high degree of correlation (LRL to DML $P < 0.001$; $r^2 = 0.98$; SE $= 0.51$); DML to weight $P < 0.001$; $r^2 = 0.99$; SE $= 0.01$) was found for both regression equations (Walker[1]). Gb-Bm DML data were log transformed and differences in DML between sample types and island were determined by comparing means with a two-sample t-test. Although the DML-weight regression is not used in the analysis, it is included here for future use by other researchers conducting bioenergetics studies.

Prey age or size estimations were limited to walleye pollock and Gb-Bm because sufficient numbers of otoliths or beaks of other primary fish and cephalopod prey species were not recovered from scat and spew samples, or because regressions for the species were unavailable.

Overlap between age classes of pollock consumed by northern fur seals and pollock caught by the commercial trawl fishery

Age-class distributions of walleye pollock in scat and spew samples were compared with pollock size-composition data in commercial midwater trawls (National Marine Fisheries Service, North Pacific Groundfish Observer Program). Trawl data included samples collected from August through September 1990 to 2000 in fishery management areas surrounding the Pribilof Islands (Berger[2]; Fig. 1) that encompass northern fur seal foraging habitat (Robson et al., 2004). Walleye pollock fork length from trawls was converted to age class by following the method of Sinclair et al. (1994) for determination of overlap with the age class of pollock consumed by northern fur seals (as estimated from scat and spew samples).

Results

Prey abundance

A total of 1127 scats and 204 spews from St. George Island and 2317 scats and 63 spews from St. Paul Island contained prey remains (Table 1). Prey species composition was similar between scats and spews for each island, but the relative importance of primary prey species based on FO% and MNI% varied by sample type and island (Table 2). Primary prey species (FO% ≥5%) found in both scats and spews consisted of gonatid group I, Gb-Bm, Gm-Gm, northern smoothtongue (*Leuroglossus schmidti*), Pacific herring (*Clupea pallasi)*, Pacific salmon (*Oncorhynchus* spp.*)*, Pacific sand lance (*Ammodytes hexapterus*), and walleye pollock (Fig. 2).

Significant interactions between sample type and island were found for Gb-Bm, Gm-Gm, Pacific salmon, and walleye pollock (Table 3); therefore the FO% of these prey was compared within island or sample type. The occurrence of Gb-Bm in scats versus spews from St. George Island was significantly different—spews having a higher FO% than scat. The FO% of Gb-Bm in scats versus spews collected from St. Paul Island was not significantly different. The FO% of walleye pollock was higher for St. George Island scats than for St. George Island spews. Pollock had the highest FO% of all prey in St. Paul Island scat and spews but was not significantly different between sample types. The FO% of Pacific salmon was significantly higher in spews than scat samples for both islands. The FO% of Gm-Gm was significantly higher in St. George Island spews than in St. Paul Island spews. Of the prey for which no interaction between sample type and island was observed, differences in the FO% of gonatid group

[2] Berger, J.   2004.   NMFS. database.   Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

Table 1

Numbers of northern fur seal (*Callorhinus ursinus*) scat and spew samples collected on St. George Island and St. Paul Island, Pribilof Islands, Alaska rookeries during the breeding season (late July–September), 1990–2000.

	St. George Island		St. Paul Island	
Year	Scats	Spews	Scats	Spews
1990	162	28	484	1
1991			109	5
1992	84	32	291	13
1993	10	1		
1994	184	46	230	3
1995	149	7	319	17
1996	141	11	337	14
1997	120	35	80	1
1998	199	24	207	5
1999			30	4
2000	78	20	230	
Total (*n*)	1127	204	2317	63

I, northern smoothtongue, and Pacific sand lance were significant between islands and between sample types (Table 3). Pacific herring was only different between islands. Year of collection had a significant effect on the occurrence of all primary prey species except gonatid group I and was included in the model as an additive variable. Although scat and spew samples were collected during the same season each year, annual comparisons between sample types were not possible because of low sample size within years (Table 1).

Variations in MNI% were observed between sample types and island for Gb-Bm and walleye pollock (Table 2). The MNI% of Gb-Bm was higher in spews than in scat samples for both islands. Conversely, the MNI% of walleye pollock was higher in scats than in spews for both islands. Scat and spew samples from St. George Island had higher MNI% of Gb-Bm than those collected from St. Paul Island. The MNI% of walleye pollock in both sample types from St. Paul Island was greater than the MNI% of walleye pollock from St. George Island in scats and spews.

Comparisons of prey age and size

A total of 1755 walleye pollock otoliths were recovered from 173 St. George Island scat samples containing walleye pollock and, of these, 1484 were determined to be in "good" or "fair" condition. Of the 152 walleye pollock otoliths recovered from 27 St. George Island spew samples, 105 were graded as "good" or "fair." From St. Paul Island, 17,827 of 20,062 walleye pollock otoliths recovered from 902 scat samples and 154 of 202 walleye pollock otoliths recovered from 23 spew samples were determined to be
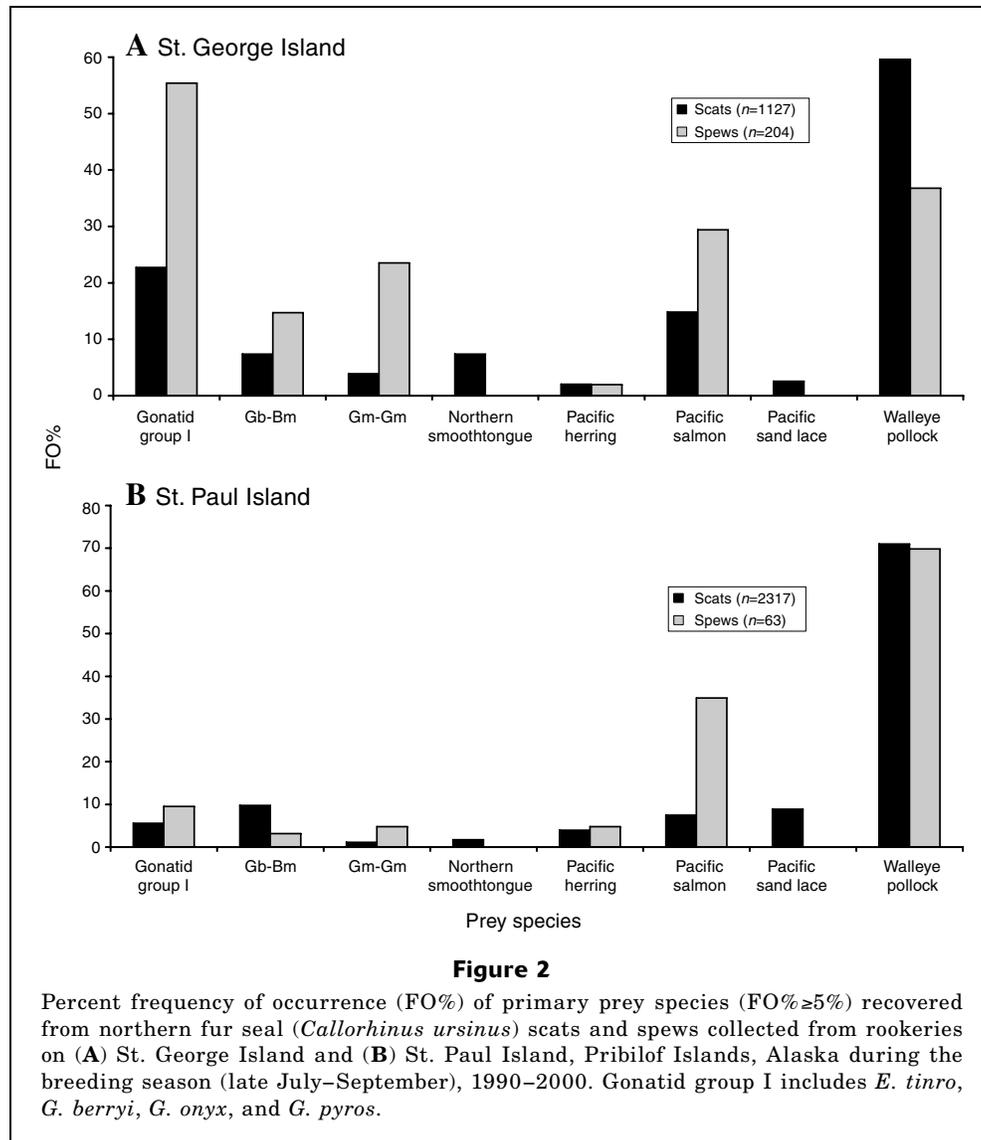
Table 2

Percent frequency of occurrence (FO%) and percent minimum number of individuals (MNI%) of prey species recovered in northern fur seal (*Callorhinus ursinus*) scat and spew samples collected on St. George Island and St. Paul Island, Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000. Table only includes prey species with an FO%≥1% within either sample type and on either island.

| Prey species | St. George Island | | | | St. Paul Island | | | |
| | FO% | | MNI% | | FO% | | MNI% | |
	Scats	Spews	Scats	Spews	Scats	Spews	Scats	Spews
Atka mackerel (*Pleurogrammus monopterygius*)	2.1	1.0	<1.0		3.6		<1.0	
Bathylagidae sp.	1.8		<1.0		<1.0		<1.0	
Gb-Bm (*Gonatopsis borealis* and *Berryteuthis magister*)	22.7	55.4	62.5	94.6	5.6	9.5	5.3	32.7
Gm-Gm (*Gonatus madokai* and *Gonatus middendorfii*)	7.4	14.7	2.8	<1.0	9.8	3.2	3.5	1.6
Gonatid group I (*E. tinro, G. berryi, G. onyx,* and *G. pyros*)	3.9	23.5	1.4	2.1	1.1	4.8	<1.0	2.0
Gonatidae sp.	1.4	1.0	<1.0	<1.0	<1.0		<1.0	
Gonatus sp.	<1.0	2.9	<1.0	<1.0	<1.0		<1.0	
Greenling sp. (*Hexagrammos* sp.)	<1.0				1		<1.0	
Northern lampfish (*Stenobrachius nannochir*)	1.0	<1.0	<1.0		<1.0		<1.0	
Northern smoothtongue (*Leuroglossus schmidti*)	7.4		5.4		1.7		1.5	
Pacific cod (*Gadus macrocephalus*)	<1		<1.0		1		<1.0	
Pacific herring (*Clupea harengus*)	2.0	2.0	<1.0		3.9	4.8	<1.0	
Pacific salmon (*Onchorhynchus* spp.)	14.8	29.4	<1.0		7.5	34.9	<1.0	
Pacific sand lance (*Ammodytes hexapterus*)	2.6		<1.0		8.9		1.1	
Pacific sandfish (*Trichodon trichodon*)	<1.0		<1.0		2	1.6	1.3	
Sablefish (*Anoplopoma fimbria*)	<1.0				1.3			
Unidentifed cephalopod	2.3	4.9	<1.0		1.2		<1.0	
Unidentified fish	27.6	3.9	<1.0		31.2		<1.0	
Unidentified gadid	17.3	15.2	<1.0		33.4	6.3	2.1	
Walleye pollock (*Theragra chalcogramma*)	59.6	36.8	22.9	2.1	71	69.8	82.3	63.3
Sample size (*n*)	(1127)	(204)	(5043)	(5754)	(2317)	(63)	(19,028)	(251)

in "good" or "fair" condition. The occurrence of walleye pollock age classes determined from otolith measurements varied by sample type (Fig. 3).

A multidimensional contingency analysis showed that sample type was independent of island ($P=0.087$, $\chi^2=6.26$, df=3); therefore data from St. George and St. Paul Islands were pooled to test for differences in age class of prey between sample types. Spews contained a larger percentage of adult pollock (88.0%, $P<0.001$, $\chi^2=260.27$, df=1) and a smaller percentage of juvenile pollock (9.1%, $P<0.001$, $\chi^2=180.91$, df=1) than scats. There was not a significant difference in the occurrence of mixed-age pollock between scats (6.4%) and spews (4.0%) ($P=0.490$, $\chi^2=0.47$, df=1) and only 71 of 1125 (6.3%) samples contained both age classes. A total of 2856 and 5030 Gb-Bm lower beaks were recovered and measured from 225 scat samples and 111 spew samples, respectively, collected at St. George Island (Fig 4.). A total of 719 Gb-Bm lower beaks were recovered and measured from 110 St. Paul Island scat samples and 47 Gb-Bm lower beaks were recovered

and measured from five St. Paul Island spew samples. The mean DML of Gb-Bm in St. George Island scat and spew samples was 69 mm (SE=0.10) and 82 mm (SE=0.14), respectively. The mean DML of Gb-Bm in St. Paul Island scat samples was 67 mm (SE=0.21) and in spew samples was 101 mm (SE=6.35). Gb-Bm data were log transformed to meet assumptions of normality for island and sample-type size comparisons. The DML of Gb-Bm estimated from beaks recovered from spew samples was significantly larger than the DML estimated from beaks recovered from scat samples collected from both islands (two-sample *t*-test, $P<0.001$ for St. George Island and St. Paul Islands). The DML of Gb-Bm from St. George Island scats was significantly larger than that form St. Paul Island scats (two-sample *t*-test, $P<0.001$). In spew samples, estimated Gb-Bm DML was significantly larger on St. Paul Island than on St. George Island (two-sample *t*-test, $P<0.001$). However, the number of spews collected from the two islands were highly unequal ($n=204$, St. George Island; $n=63$, St. Paul Island).

Figure 2

Percent frequency of occurrence (FO%) of primary prey species (FO%≥5%) recovered from northern fur seal (*Callorhinus ursinus*) scats and spews collected from rookeries on (**A**) St. George Island and (**B**) St. Paul Island, Pribilof Islands, Alaska during the breeding season (late July–September), 1990–2000. Gonatid group I includes *E. tinro*, *G. berryi*, *G. onyx*, and *G. pyros*.

Overlap between age classes of pollock consumed by northern fur seals and pollock caught by the commercial trawl fishery

The percent overlap between age classes of walleye pollock caught by the commercial trawl fishery and those consumed by northern fur seals varied between sample types for both islands. Minimal overlap was observed between age classes of pollock found in St. George Island and St. Paul Island scats and those taken by the commercial trawl fishery (St. George Island=15.5%; St. Paul Island=4.1%, Fig. 3). However, the percentage of overlap between age classes of pollock found in St. George Island and St. Paul Island spews and the age classes of pollock taken in commercial trawls was considerable (St. George Island=94.6%; St. Paul Island=89.6%, Fig. 3).

Discussion

Northern fur seal diet studies conducted since the 1980s have primarily used scat samples to determine prey species and size. Despite the presence of spews on rookery and haul-out beaches, only Kiyota et al. (1999) has utilized spews to study northern fur seal diet. Kiyota et al. (1999) examined spews and scats collected from haul-outs (subadult male dominated) and found differences in the prey remains recovered between sample types. We compared the diet of adult female northern fur seals using scats and spews collected from rookeries on the Pribilof Islands over an eleven-year period. We observed differences in the percent frequency of occurrence (Fig. 2) and the estimated age or size (Figs. 3 and 4) of prey between scats and spews. Additionally, the degree of overlap between age classes of walleye pollock consumed by northern fur seals and those caught in

commercial fishery trawls varied considerably by sample type (Fig. 3). These findings highlight the potential limitations of a single sample type, such as scats, and demonstrate that a combination of scat and spew samples can provide a more complete description of northern fur seal diet.

The differences in prey occurrence that were observed among northern fur seal scats and spews in our study may have resulted from the accumulation of irregularly shaped or large prey parts in the stomach (Kiyota et al., 1999). Large cephalopod beaks and fish bones accumulate near the pyloric sphincter and are regurgitated from the stomach, whereas small prey parts pass through the digestive system and are recovered in scats (Bigg and Fawcett, 1985). The different rates of retention of prey parts in northern fur seal stomachs would, therefore, bias scat samples toward small prey species or small bones of large prey species and spew samples toward large prey and cephalopods. For example, the FO% of Pacific salmon, a large boned fish species, was higher in spews than in scats. Kiyota et al. (1999) also observed a higher occurrence of Pacific salmon in spews than in scats of juvenile male northern fur seals from St. Paul Island. The FO% we observed for northern smoothtongue and Pacific sand lance also support a prey species bias between sample types; the small forage fish were among primary prey species found in scat samples but were absent from spew samples.

In addition to differences observed between sample types, we found that the occurrence of primary prey species varied between islands. Specifically, the FO% of gonatid group I, Gb-Bm, Gm-Gm, and walleye pollock varied considerably between sample types and islands, and significant interactions between sample type and island were observed for a number of these species. Walleye pollock was the highest occurring prey in St. George Island scats, but the FO% was significantly lower in spew samples. On St. Paul Island, walleye pollock was the dominant prey species, but the FO% did not differ between scats and spews. Similarly, the FO% of Gb-Bm at St. Paul Island did not differ between sample types. However, the FO% of Gb-Bm was significantly higher in spews than in scats on St. George Island. The FO% of gonatid group I differed both between sample types and between islands; the occurrence of this group was highest in spews, and in samples from St. George Island. Overall, cephalopods occurred at higher frequencies on St. George Island than on St. Paul Island for both sample types. The lone exception was Gm-Gm, which had a lower frequency on St. George Island for scats. Observed differences in cephalopod and walleye pollock occurrence between St. George
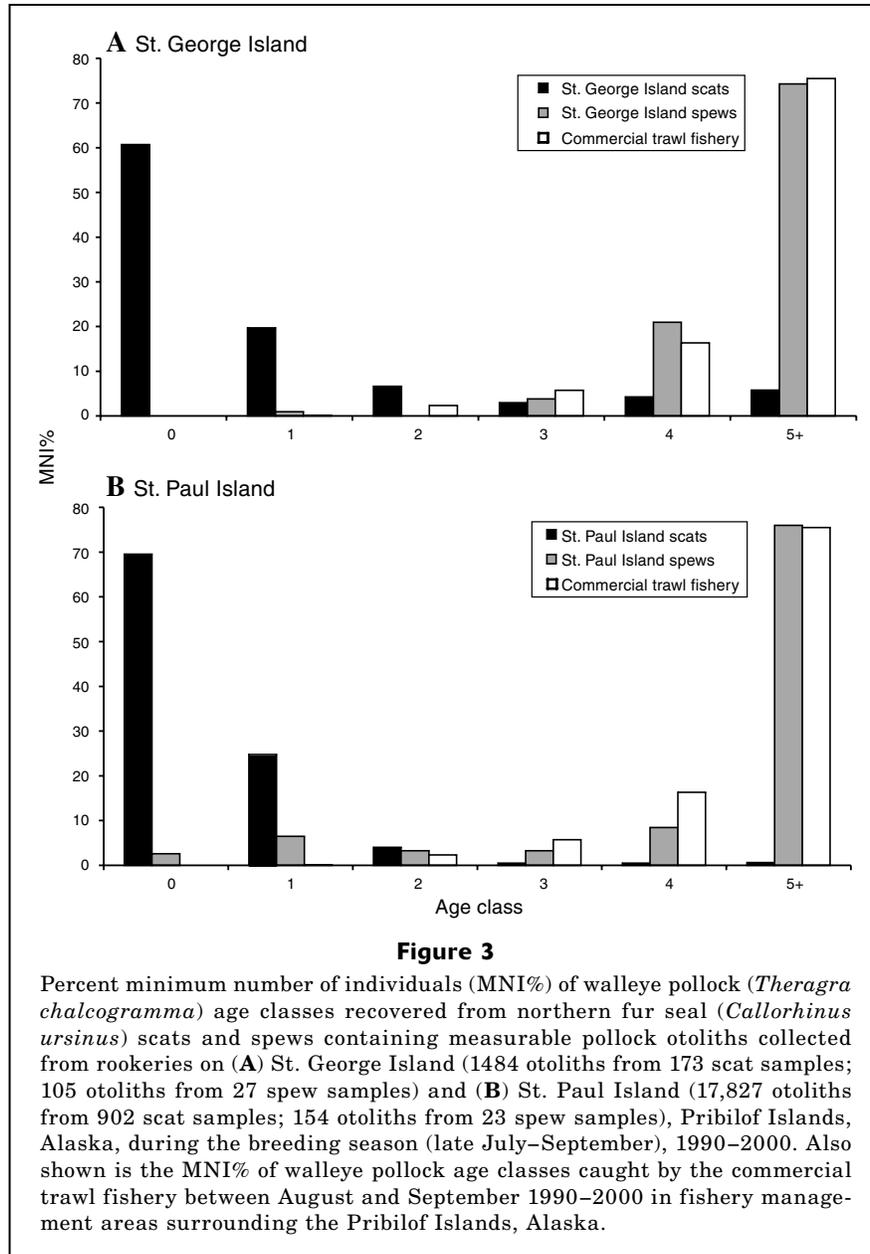
Table 3

Results of generalized linear model comparing occurrence of primary prey species identified in northern fur seal (*Callorhinus ursinus*) scat and spew samples collected on St. George Island and St. Paul Island, Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000. The following abbreviations are used for cephalopod prey: Gb-Bm (*Gonatopsis borealis* and *Berryteuthis magister*), Gm-Gm (*Gonatus madokai* and *Gonatus middendorfii*), and gonatid group I (*Eogonatus tinro*, *Gonatus berryi*, *G. onyx*, and *G. pyros*).

Prey	Year			Interaction (island × sample type)			Islands (St. Paul and St. George)			Sample type (scat and spew)		
	χ^2	df	P	χ^2	df	P	χ^2	df	P	χ^2	df	P
Gb-Bm	47.18	10	<0.0001	4.12	1	0.0424		—		1.95	1	0.1625 St. Paul only
										91.42	1	<0.0001 St. George only
Gm-Gm	118.14	10	<0.0001	8.37	1	0.0038	0.78	1	0.3771 scats only		—	
							3.84	1	0.0500 spews only		—	
Gonatid group I	17.31	10	0.0678	0.74	1	0.3908	40.12	1	<0.0001	78.10	1	<0.0001
Northern smoothtongue	70.25	10	<0.0001	0.00	1	0.9862	44.18	1	<0.0001	25.29	1	<0.0001
Pacific herring	90.37	10	<0.0001	0.03	1	0.8709	6.26	1	0.0124	0.10	1	0.7559
Pacific salmon	97.94	10	<0.0001	9.70	1	0.0018		—		37.81	1	<0.0001 St. Paul only
										19.59	1	<0.0001 St. George only
Pacific sand lance	57.77	10	<0.0001	0.00	1	0.9887	56.98	1	<0.0001	19.00	1	<0.0001
Walleye pollock	199.41	10	<0.0001	11.94	1	0.0005		—		0.29	1	0.5921 St. Paul only
										41.46	1	<0.0001 St. George only

Figure 3

Percent minimum number of individuals (MNI%) of walleye pollock (*Theragra chalcogramma*) age classes recovered from northern fur seal (*Callorhinus ursinus*) scats and spews containing measurable pollock otoliths collected from rookeries on (**A**) St. George Island (1484 otoliths from 173 scat samples; 105 otoliths from 27 spew samples) and (**B**) St. Paul Island (17,827 otoliths from 902 scat samples; 154 otoliths from 23 spew samples), Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000. Also shown is the MNI% of walleye pollock age classes caught by the commercial trawl fishery between August and September 1990–2000 in fishery management areas surrounding the Pribilof Islands, Alaska.
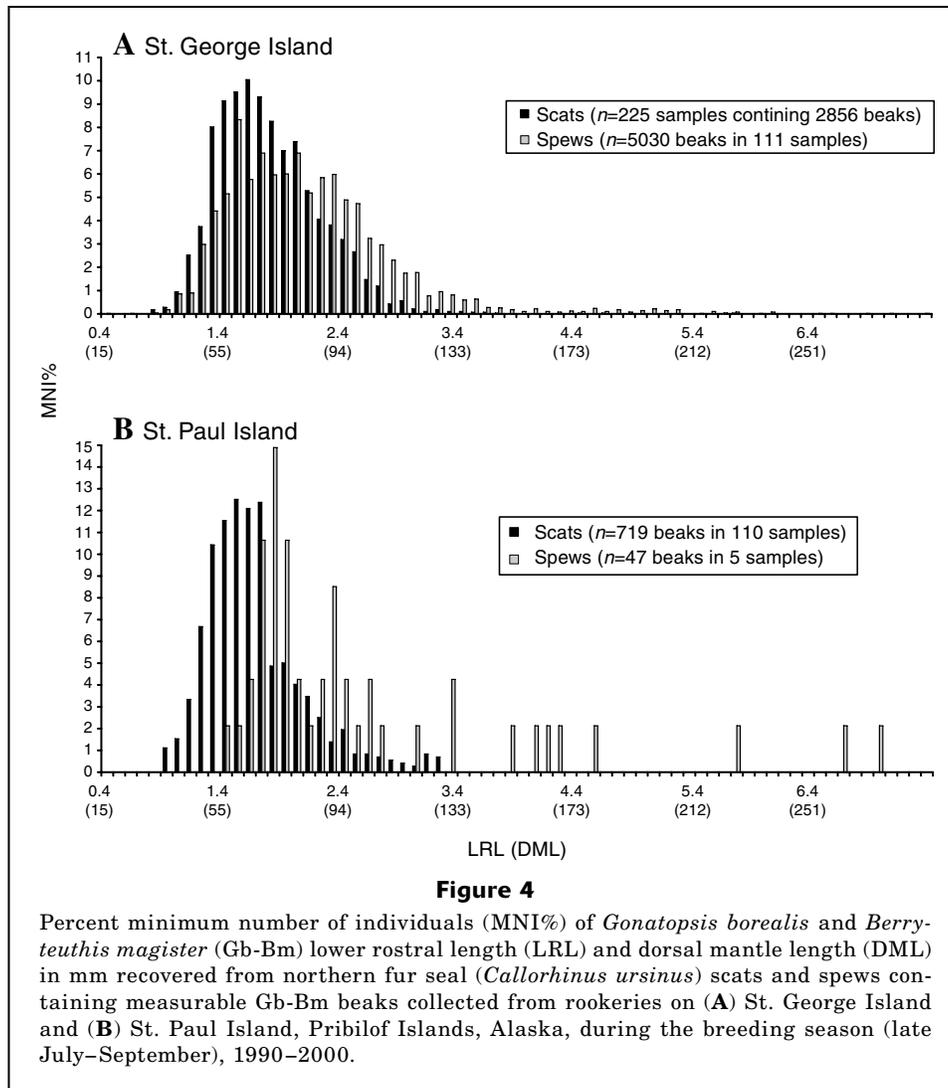
Island and St. Paul Island samples are likely related to the availability of prey within reach of female fur seals, which varies according to the physical and biological environment surrounding each island (Sinclair et al., 1994; Antonelis et al., 1997; Robson et al., 2004).

The occurrence of important prey species in scat samples was consistent with previous analyses of northern fur seal scat and stomach samples. However, there were considerable differences in prey occurrence between spews samples and previous studies (Kajimura, 1984; Sinclair et al., 1994, 1996; Antonelis et al., 1997). In northern fur seal diet studies based on analysis of the entire gastrointestinal tract adult females were found to primarily consume juvenile walleye pollock and gonatid

squid (Sinclair et al., 1994; 1996). Likewise, diet studies based on scat samples had the highest occurrences of walleye pollock and gonatid squid (Antonelis et al., 1997). Although we observed a similar FO% of walleye pollock in our scat samples, the FO% of gonatid squid and Pacific salmon were significantly higher among spews compared to previous studies based on scat and G.I. tract samples. Thus, it is likely that the importance of some prey species, such as gonatid squids and Pacific salmon, has been underestimated in previous diet studies (e.g., Antonelis et al., 1997).

Significant differences in the size of Gb-Bm were observed between scat and spew samples, demonstrating size-related digestive biases between sample types.

Figure 4

Percent minimum number of individuals (MNI%) of *Gonatopsis borealis* and *Berry-teuthis magister* (Gb-Bm) lower rostral length (LRL) and dorsal mantle length (DML) in mm recovered from northern fur seal (*Callorhinus ursinus*) scats and spews containing measurable Gb-Bm beaks collected from rookeries on (**A**) St. George Island and (**B**) St. Paul Island, Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000.

The dorsal mantle length size of Gb-Bm estimated from lower beaks was significantly larger in spew samples than scat samples (Fig. 4). Digestive biases relating to cephalopod beak size have also been observed in northern fur seal G.I. tracts (Yonezaki et al., 2003), as well as in Australian fur seal (*Arctocephalus pusillus doriferus*; Gales et al., 1993) and California sea lion (*Zalophus californianus*; Lowry and Carretta, 1999) spews and scats. Owing to limited taxonomic resolution of squid species in previous northern fur seal diet studies, direct comparisons of Gb-Bm size were not possible. For instance, Sinclair et al. (1994) presented DML size ranges of beaks recovered from stomachs, but, the cephalopod groups Gb-Bm and Gm-Gm were combined for analysis and were reported as gonatid squid.

We observed a greater percentage of adult walleye pollock in spew than in scat samples (Fig. 3). In addition, few scat and spewing samples were found to contain otoliths from both juvenile and adult age categories, further demonstrating size-related digestive biases of prey remains between sample types. The differences in walleye pollock age classes between scat and spew samples seem to indicate that size estimations of pollock consumed by northern fur seals have likely been underestimated in previous studies using G.I. tracts and scats (Sinclair et al., 1994, 1996). Northern fur seal diet studies based on analysis of the entire G.I. tract have shown that adult females consume primarily juvenile walleye pollock (Sinclair et al., 1994, 1996). However, biases associated with the retention of large prey remains are inherent in studies based on G.I. tract samples (Pierce and Boyle, 1991; Gales et al., 1993), and size-selective relationships between prey otolith size and sample type have been documented for northern fur seals (Kiyota et al., 1999; Yonezaki et al., 2003).

Data that accurately describe the ages of walleye pollock consumed by northern fur seals are critical for assessing potential competition with the commercial trawl fishery, which focuses on adult pollock. Previous northern fur seal diet analyses using scat and G.I tract

samples have revealed that northern fur seals primarily consume juvenile walleye pollock (Sinclair et al., 1994, 1996), indicating that there is limited competition between northern fur seals and the commercial trawl fishery. When walleye pollock age class was estimated from scats collected from 1990 to 2000, we found minimal overlap between the age classes of pollock consumed by northern fur seals and age classes of pollock caught by the commercial fishery during this time (Fig. 3). However, when spew samples were used to estimate age/size of fur seal prey, a high degree of overlap between age classes of pollock consumed by northern fur seals and pollock caught by the commercial fishery was observed (Fig. 3).

Because of the protective measures that resulted in closures of fisheries in Steller sea lion (*Eumetopias jubatus*) critical habitat, there is concern that fishery pressures in waters surrounding the Pribilof Islands may increase (NMFS[3]). Approximately 75% of the global northern fur seal breeding population inhabits the Pribilof Islands during the summer months (Loughlin et al., 1994) and recent estimates indicate a population decline. The total number of adult males on St. George and St. Paul Islands decreased by 13.4% and 2.8%, respectively, from 2002 to 2003 (Towell et al., 2006; York et al., 2005). Pup production also declined by >5% per year between 1998 and 2002 on both islands (York et al., 2005). At present, the cause of decline is uncertain but there is concern that increased fishing activity in waters surrounding the Pribilof Islands may adversely affect the northern fur seal population. We found that the occurrence and the age or size of some important prey species (such as walleye pollock) has been underestimated in previous northern fur seal diet studies in which only scat samples were used. Because some of these species are also commercially important, northern fur seal conservation and fishery management decisions should incorporate diet-related information acquired from multiple noninvasive sampling methods. This approach would allow better interpretation of northern fur seal dietary requirements, thereby providing a more accurate estimation of the extent to which protective measures in and around the Pribilof Islands should be instituted.

Scat and spew samples were collected simultaneously from the same rookeries on the Pribilof Islands during the breeding season; therefore we do not believe our results were affected by sampling effort. The discrepancies in sample sizes observed in this study may be the result of northern fur seal foraging behavior. Satellite tracking and behavioral studies of female northern fur seals have indicated that individual at-sea foraging trips may range between 6 and 10 days on average (Loughlin et al., 1987; Gentry, 1998; Robson et al., 2004). The accumulation of large cephalopod beaks and

fish bones near the pyloric sphincter during this time may have irritated the stomach, causing the fur seals to regurgitate prey remains while at sea prior to their return to the rookeries. Although we do not know the regurgitation rates of fur seals, a tendency to regurgitate food during active digestion would explain the differences in sample size between spew and scat samples found on rookeries of the Pribilof Islands. Differences in proportions of sample types also have been observed on northern fur seal haul-outs (Kiyota et al., 1999), as well as on California sea lion haul-outs (Lowry and Carretta, 1999) and on Australian fur seal rookeries and haul-outs (Gales et al., 1993). Despite the skewed sample sizes between scats and spews in the present study, the observed differences in FO% and estimated age or size of prey between sample types were similar for both islands and were consistent with previous pinniped diet studies comparing scat and spew samples (e.g., Gales et al., 1993, Kiyota et al., 1999).

The various sampling methods used in pinniped diet analyses each have associated biases and sources of error that must be considered. The reliance upon any one sample type in diet assessments will limit one's ability to completely describe prey composition and prey size. Although our results corroborate the findings of previous diet studies with regard to the primary prey consumed by northern fur seals, this study demonstrates that using multiple sampling methods allows for a more accurate assessment of occurrence and age or size of prey.

Acknowledgments

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