

Abstract—Along the west coast of the United States, the potential impact of increasing pinniped populations on declining salmonid (*Oncorhynchus* spp.) stocks has become an issue of concern. Fisheries managers need species-specific estimates of consumption by pinnipeds to evaluate their impact on salmonid stocks. To estimate consumption, we developed a model that estimates diet composition by reconstructing prey biomass from fecal samples. We applied the model to data collected from harbor seals (*Phoca vitulina*) that are present year-round in the lower Columbia River where endangered stocks of salmonids pass as returning adults and as seaward-migrating smolts. Using the same data, we applied the split-sample frequency of occurrence model, which avoids reconstructing biomass by assuming that each fecal sample represents an equal volume of consumption and that within each sample each prey item represents an equal proportion of the volume. The two models for estimating diet composition yielded size-specific differences in consumption estimates that were as large as tenfold for the smallest and largest prey. Conclusions about the impact of harbor seal predation on adult salmonids, some of their largest prey species, remain uncertain without some appropriate rationale or further information (e.g. empirical captive studies) to discriminate between these models.

Pinniped diet composition: a comparison of estimation models

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During the last three decades, harbor seal (*Phoca vitulina*) and California sea lion (*Zalophus californianus*) populations along the west coast of the United States have increased dramatically (Forney et al., 2000). During the same period, numerous salmonid (*Oncorhynchus* spp.) stocks that are consumed by these pinnipeds have declined and some of these stocks have been classified as threatened or endangered (NMFS, 1997). To evaluate the impact of pinnipeds, fisheries managers need species-specific estimates of salmonid consumption by pinnipeds.

In some limited situations, pinniped prey consumption can be determined from direct observation if the pinniped brings the prey to the surface and feeding occurs in a few predictable areas (Bigg et al., 1990). However, in most situations, consumption estimates have relied on a less direct approach that uses estimates of pinniped energetic requirements, prey energy density, and pinniped diet composition (Olesiuk, 1993; Hammill et al., 1997; Stenson et al., 1997; Nilssen et al., 2000). In their simplest form, these models express biomass consumption of prey species i as $B_i = \xi \pi_i / \epsilon_i$, where ξ is the total energy requirement of the pinnipeds, π_i is the proportion of the energy in the diet derived from species i , and ϵ_i is the energy density (kcal/g) of species i . The total energy requirement of a population depends on the size of the population and requirements of each seal, which vary by sex, age, and status (i.e.

whether it is molting, pregnant, lactating). If prey energy density is constant or an average energy density is used, biomass consumption can be expressed as $B_i = \xi \pi_i$, where ξ is the total biomass requirement and π_i is the proportion of the biomass derived from species i . Valid estimates of pinniped energetic requirements and prey energy density are important, as well as accurate estimates of pinniped diet composition.

Diet composition can be determined from skeletal remains in scat (feces) and from stomach and intestinal contents, or stomach lavage. Each of these methods has some inherent bias (Bigg and Perez, 1985; Pierce et al., 1991). Examination of prey remains in scat is noninvasive and allows for the largest sample size. There are, however, numerous well-recognized problems in describing marine mammal diet from scats (Jobling, 1987; Harvey, 1989; Harvey and Antonelis, 1994; Tollit et al., 1997b; Marcus et al., 1998). In particular, nonrandom passage of hard parts, primarily otoliths, biases estimates of diet composition; however, the bias can be reduced by inclusion of all hard parts (e.g. bones) (Browne et al., 2002).

In 1994, we began an investigation of harbor seal consumption of salmonids in the lower Columbia River. Initial attempts to survey the lower 110 km stretch of the river to estimate adult salmonid consumption by direct observation proved infeasible. The only remaining noninvasive alternative was to develop a consumption estimate

based on analysis of scat collections. During 1995–97, harbor seal scats were collected at the Desdemona Sands haulout from 1 March to 15 October. By combining diet composition obtained from scat analysis and contemporaneous surveys of seal abundance, we estimated the average consumption of salmonids and other prey in the Columbia River by harbor seals during spring, summer, and fall of 1995–97.

In our study, we focussed on the method of estimating diet composition from a sample of scats. We describe an estimator for diet composition based on reconstruction of the prey biomass represented in the scat and show how it is related to an alternative estimator described by Olesiuk (1993). Using the data collected on harbor seals in the Columbia River, we demonstrate the sensitivity of the consumption estimates to the method for estimating diet composition.

Materials and methods

Diet composition models

If we could randomly select a sample of n prey items consumed by pinnipeds, a ratio estimator (Cochran, 1977) would be appropriate to estimate the proportion of biomass (π_i) represented by the i^{th} prey species from ω possible prey species:

$$\hat{\pi}_i = \frac{b_i}{\sum_{i=1}^{\omega} b_i} = \frac{n_i \bar{w}_i}{\sum_{i=1}^{\omega} n_i \bar{w}_i}, \quad (1)$$

where b_i = the total biomass of the n_i prey items that are species i ;

$\bar{w}_i = b_i/n_i$ = the average mass for species i ; and

$$n = \sum_{i=1}^{\omega} n_i.$$

Prey hard-parts in a scat represent a filtered selection of the prey species that were consumed by a single animal over some unknown and variable amount of time. Captive feeding studies have shown that a scat does not represent a single meal or even a single fixed period of feeding time (Harvey, 1989). Moreover, pinnipeds are unlikely to consume the same amount of prey in each meal or in a specified amount of time. Therefore, the biomass represented by the prey remains in a scat is unlikely to be constant because consumption varies. From a collection of s scats in which each scat represents a variable amount of biomass that is proportional to consumption, the ratio estimator (Eq. 1) is also appropriate, where b_i is the total biomass of species i from the s scats. We will refer to (Eq. 1) as biomass reconstruction (BR), which is equivalent to the estimator used by Harvey (1988) and Hammond and Rothery (1996).

Alternatively, one could argue that the biomass reconstructed from prey remains in a scat may vary for numerous reasons other than consumption. Variation in scat volume and production and the resulting amount of hard

parts may be affected by factors that influence digestion and deposition (e.g. seal activity level). Also, it may not always be possible to collect an entire scat or even reasonably define a scat as a discrete entity. Thus, even though consumption by seals varies to some degree, the biomass reconstructed from a scat may vary much more than the variation in consumption. Thus, one could argue that each scat should be treated as a “representative” variable-size sample of a nearly constant amount of biomass consumed during some feeding interval. With that conceptual sampling model, the most appropriate estimator would be a simple average of the proportions in each scat:

$$\hat{\pi}_i = \frac{\sum_{k=1}^s \hat{\pi}_{ik}}{s} = \frac{\sum_{k=1}^s \left(\frac{b_{ik}}{\sum_{i=1}^{\omega} b_{ik}} \right)}{s} = \frac{\sum_{k=1}^s \left(\frac{n_{ik} \bar{w}_{ik}}{\sum_{i=1}^{\omega} n_{ik} \bar{w}_{ik}} \right)}{s} \quad (2)$$

where b_{ik} = the biomass of species i ;

n_{ik} = the number of species i consumed; and

\bar{w}_{ik} = the average mass of species i in the k^{th} scat.

Equation 2 is similar to the estimator of Olesiuk (1993), which he called split-sample frequency of occurrence (SSFO):

$$\hat{\pi}_i = \frac{\sum_{k=1}^s \left(\frac{I_{ik}}{\sum_{i=1}^{\omega} I_{ik}} \right)}{s}, \quad (3)$$

where I_{ik} = an indicator variable which equals 1 if one (or more) prey items of species i is in scat k , and 0 otherwise.

Equation 2 is equivalent to 3 when you make Olesiuk’s (1993) assumption that an equal amount of biomass of each species in the scat was consumed. SSFO requires only a determination of the presence or absence of the prey in a scat, and thus, it is much easier to implement than either Equations 1 or 2, which require an enumeration of the individual prey in each scat and their mass.

Enumeration of prey in a scat sample is straightforward with unique structures such as otoliths. However, by using nonunique hard parts (e.g. gillrakers, vertebrae) to reduce selection bias resulting from unequal digestibility of otoliths, problems are introduced with enumeration. When prey are exclusively represented in scat by nonunique structures, it may be possible only to determine that a single individual was consumed or at best a minimum number can be constructed by enumerating nonunique structures and dividing by the average number of structures per fish (e.g. count of vertebrae divided by average number of vertebrae per fish). By including nonunique structures, enumeration of prey is replaced with an estimate of the

minimum number of prey (\hat{n}_i) consumed. For some hard parts, it may not be possible to identify the species, but the hard part can be classified to a group of species, such as family. In these cases, the species can be grouped into a single unit for estimation (e.g. all hexagrammids) or the unidentified prey can be partitioned to species based on the sample of species-specific hard parts. For example, most salmonid bones are currently indistinguishable to species; therefore salmonids in scats represented by bones (u) can be apportioned into species from proportions (γ_i) observed from otoliths (o_i). If we denote Ψ to be the set of all identified salmonids represented by otoliths, the number of salmonid prey in species i can be estimated as

$$\hat{n}_i = o_i + u\hat{\gamma}_i \quad \text{for } i \in \Psi, \quad (4)$$

where

$$\hat{\gamma}_i = \frac{o_i}{\sum_{i \in \Psi} o_i} \quad \text{for } i \in \Psi, \quad (5)$$

Prey mass can be determined from morphometric relationships between hard part dimensions (e.g. typically otolith length) and mass. Adjustments should be made to account for partial digestion of the hard part. From regressions between otolith length (corrected for degradation) and fish length and between fish length and mass, an estimate of the average mass of prey represented in scat can be constructed (Harvey et al., 2000; Browne et al., 2002). In some scats, a prey species may be represented only by hard parts (e.g. gillrakers) that do not have a quantifiable relationship to mass. We have to assume that the prey with unknown mass are represented by the average mass determined from the measurable hard parts (e.g. unbroken otoliths) of that species.

Thus, the biomass cannot strictly be measured but must be estimated by using estimated average mass (\bar{w}_i) and estimated number of individual prey (\hat{n}_i):

$$\hat{b}_i = \hat{n}_i \frac{\sum_{j=1}^{o_i^*} \hat{w}_{ij}}{o_i^*} = \hat{n}_i \bar{w}_i, \quad (6)$$

where o_i^* = the number of hard parts (typically unbroken otoliths); and

\hat{w}_{ij} = the estimated mass derived from the regressions relating otolith length to fish mass.

To estimate number of prey consumed (P_i) rather than biomass, estimated biomass is divided by average mass:

$$\hat{P}_i = \frac{\hat{B}_i}{\bar{w}_i} = \xi \frac{\hat{\pi}_i}{\bar{w}_i} = \xi \hat{\rho}_i, \quad (7)$$

where $\hat{\rho}_i = \frac{\hat{n}_i}{\sum_{r=1}^{\omega} \hat{b}_r}$ = the number of prey species i consumed per unit of biomass consumed.

Pinniped diet can be quite variable in response to prey availability (Pierce et al., 1991; Tollit et al., 1997a; Browne et al., 2002; Beach et al.¹; Brown et al.²). Because scat collected at a single date may reflect what was locally available at that time, collecting scats at different times throughout a season or year will provide a better representation of diet. From scats collected across several occasions, what is the best way to estimate average diet composition? If the amount of scat collected and resulting reconstructed biomass for an occasion is proportional to the amount of prey consumed, the data should be pooled for a single ratio estimate. However, in many cases the amount of scat collected will reflect a multitude of factors, such as tide height, storms, human disturbance, and the length of time that the seals were at the haulout prior to collection. Also, in many circumstances a fixed number of scats are collected rather than some fixed proportion of the scats available at the haulout. Therefore, we suggest that an average of the proportions (ratios) is appropriate. If there are T occasions, the average proportion is

$$\hat{\pi}_i = \frac{\sum_{t=1}^T \hat{\pi}_{it}}{T}. \quad (8)$$

Often there are seasonal shifts in diet resulting from prey availability (Olesiuk et al., 1990; Tollit and Thompson, 1996; Browne et al., 2002). In such cases, the analysis should be stratified by season. If data are collected over several years, again a simple average of the seasonal proportions is appropriate. In the appendix, we provide variance estimators for diet composition and consumption estimates for data collected over several years stratified by season.

Data collection and analysis

For the data used in this paper, Browne et al. (2002) have described the scat collection and analytical methods and have provided descriptions of the food habits from these data. As in Browne et al. (2002), we stratified our data collection and analysis into three seasons, spring (1 March–14 May), summer (15 May–15 July) and fall (16 July–15 October), based on the timing of chinook salmon runs at the Bonneville Dam, offset by two weeks to account for the travel of salmonids from the lower Columbia River to the Dam (at river km 235). We describe here additional meth-

¹ Beach, R. J., A. C. Geiger, S. J. Jefferies, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982. NWAFC Processed Rep. 85-03, 316 p. Northwest and Alaska Fisheries Sci. Cent., Nat. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

² Brown, R. F., S. D. Riemer, and S. J. Jefferies. 1995. Food of pinnipeds collected during the Columbia River Area Commercial Salmon Gillnet Observation Program, 1991–1994. Wildlife Diversity Program Tech. Rep. 95-6-01, 16 p. Oregon Department of Fish and Wildlife, 2501 SW 1st Ave., PO Box 59, Portland, OR 97207.

ods for development of estimates of prey consumption by harbor seals.

Prey remains were usually identified to species, but in some cases could only be identified to genus, family, or larger taxon (e.g. flatfish). Our primary interest was salmonid consumption; therefore, where possible, we also classified salmonids as juvenile or adult. For non-salmonids, we were less interested in species-specific estimates of consumption; therefore we did not always identify nonotolith remains to species when identification was either time-consuming or uncertain. For example, we divided flatfish into starry flounder (*Platichthys stellatus*) and “other flatfish” because starry flounder were easily identified, but the remaining flatfish species were not easily distinguishable. In some cases, prey remains could be identified to species, but they occurred infrequently; therefore we grouped them by family (e.g. Hexagrammidae) or groups of families (e.g. Stichaeidae and Pholididae). We have used the term “prey group” to generically refer to our classification of prey remains into family (or more general taxon), species, or species and size.

Both species and size of salmonids could be determined from unbroken otoliths. For most salmonids, even broken otoliths were classified as adult or juvenile because of a very apparent discontinuity in otolith size between adults and juveniles. However, for coho salmon (*O. kisutch*) and cutthroat trout (*O. clarkii*), the size difference between juveniles and adults was less obvious; therefore we did not classify broken otoliths. We partitioned coho salmon and cutthroat trout broken otoliths into adults and juveniles according to the observed seasonal proportion of unbroken otoliths for each species. Salmonids represented exclusively by bone were not separated by species or size, but were apportioned according to seasonal average proportions measured from otoliths.

The lengths of all unbroken otoliths were measured to compute an average mass for most prey. We corrected the measured length for an average amount of degradation (Browne et al., 2002). For Pacific mackerel (*Scomber japonicus*), elasmobranchs (sharks and skates), lamprey (*Petromyzontid* spp.) and peamouth chub (*Mylocheilus caurinus*), size relationships were not available; therefore literature values of average mass were used (Browne et al., 2002). For many species, there were very few measurable otoliths for an individual collection date; therefore an average weight was computed across all collection dates within that particular season and applied to each collection date during that season. If there were 10 or fewer hard parts measured in each season, we used the average and variance of the predicted weights from the data pooled over the three seasons (i.e. we assumed no seasonal differences).

The amount of prey biomass (ξ) required to sustain the harbor seals in the Columbia River during a season is a function of seal abundance (N), the age and sex proportions (θ_a) and the sex- and age-specific daily biomass requirements of the seals (C_a), and the length of the season (D):

$$\xi = N \sum_a \theta_a C_a D. \quad (9)$$

We confined our analysis to nonpup (>6 months) seals because weaned pups comprise a small proportion of the seals in the Columbia River and they primarily consume soft-bodied prey or crustaceans (Pitcher, 1980; Riemer and Brown³) which could not be incorporated into our estimates of diet composition. The average number of seals was determined from aerial surveys that were flown over seal haulout sites. Pups and nonpups were counted from photographic slides or they were counted during flights over small haulout sites. Aerial surveys were flown on 10 occasions between March and July 1995, on 16 occasions between March and June 1996, and on 25 occasions between March and September 1997. In 1997, radio-tags and visual markers were attached to 26 seals (8 adult males, 10 adult females, and 8 subadults) to estimate the average proportion of nonpup seals that were hauled out during the surveys (f) with the techniques described by Huber et al. (2001). The correction factor was used for all of the counts to construct average seasonal abundance estimates. Abundance of nonpup seals in each season was estimated by

$$\hat{N}_j = \frac{\bar{c}_j}{f}, \quad (10)$$

where \bar{c}_j = the average count of nonpup seals hauled out during season j .

Age (other than unmolted pups) and sex of seals cannot be determined from aerial surveys; therefore, estimating the sex and age structure would require capturing seals at different times throughout the year. Instead, we relied on a predicted sex and age structure based on life-history table data (Bigg, 1969; Pitcher and Calkins⁴), but rescaled the proportions to the nonpup portion of the population. We used the following sex and age structure for nonpup seals (θ_a): $a=1$, 23% subadult (1–4 yr); $a=2$, 35% adult males (>4 yr); $a=3$, 42% adult females (>4 yr). We assumed the following biomass requirements for the three groups: $C_1=1.89$ kg/d, $C_2=2.37$ kg/d, and $C_3=2.63$ kg/d. We derived these values by averaging the age-specific daily biomass requirements given by Olesiuk (1993). We did not include any variability in our estimates of biomass requirements, nor did we include any uncertainty in the estimates of the population structure (θ_a). Therefore, variability in ξ only included variation in the population estimate.

³ Riemer, S. D., and R. F. Brown. 1997. Prey of pinnipeds at selected sites in Oregon identified by scat (fecal) analysis, 1983–1996. Wildlife Diversity Program Tech. Rept. 97-6-02. 34 p. Oregon Department of Fish and Wildlife, 2501 SW 1st. Ave., PO Box 59, Portland, OR 92707.

⁴ Pitcher, K. W., and D. G. Calkins. 1979. Biology of the harbor seal, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. Final Rep. to OCSEAP (Outer Continental Shelf Environmental Assessment), Dept. Interior, Bur. Land Manage., 72 p.

Table 1Apportionment of unidentified salmonid remains based on proportions of identified salmonid remains as species i in season j (γ_{ij}).

Species	Age class	Proportions (γ_{ij})			Apportioned unidentified ($\gamma_{ij}u_j$)		
		Spring	Summer	Fall	Spring	Summer	Fall
Chinook	Adult	0.038	0.083	0.462	2.3	2.3	30.9
	Juvenile	0.538	0.389	0.077	31.8	10.9	5.2
Coho	Adult	0.051	0.292	0.231	3.0	8.2	15.5
	Juvenile	0.026	0.000	0.154	1.5	0.0	10.3
Cutthroat	Adult	0.144	0.049	0.000	8.5	1.4	0.0
	Juvenile	0.144	0.146	0.077	8.5	4.1	5.2
Sockeye	Adult	0.019	0.000	0.000	1.1	0.0	0.0
Steelhead	Adult	0.019	0.014	0.000	1.1	0.4	0.0
	Juvenile	0.019	0.028	0.000	1.1	0.8	0.0
Total (u_j)					59	28	67

Table 2Average and coefficient of variation (in parentheses) of the count (\bar{c}_j) of hauled-out nonpup seals, estimated abundance (N_j) and prey biomass requirements (ξ_j) for each season.

Season	Avg. count	Abundance	Required biomass (t)
Spring (1 Mar–14 May)	1012 (0.11)	1659 (0.12)	296.34 (0.12)
Summer (15 May–15 July)	823 (0.07)	1349 (0.10)	193.65 (0.10)
Fall (16 July–15 Oct)	598 (0.15)	980 (0.16)	214.21 (0.16)

Results

Scats were collected on 31 occasions during March–October 1995–97 providing 1385 scats with identifiable prey remains (Browne et al., 2002). All seasons were sampled in each year except for the fall of 1995. Remains were identified from 5832 different prey which were assigned to $\omega=28$ prey groups. We excluded the very minor unidentified component. Salmonids of unknown species and size represented by bone (154) were partitioned based on the observed seasonal proportions (Eqs. 4 and 5, Table 1).

During 16 of the flights in 1997, the proportion of the 26 radio-tagged seals hauled out was measured to construct a single average correction factor ($1/f$) of 1.64 (percent coefficient of variation (CV)=6.7%) to estimate seasonal abundance from the haulout counts (Table 2). Using the assumed age and sex structure and biomass requirements, we estimated that the seals in the Columbia River would consume 704 metric tons (t) of biomass during the 7.5 month period (Table 2).

From the 1385 scats, we reconstructed 1.15 t of biomass which was only 0.16% of the required biomass consumption. Because the number of scats and seals varied between seasons, the percentages varied from 0.077% in spring, 0.173% in summer, and 0.272% in fall. Using BR,

we constructed diet composition estimates (Fig. 1) and seasonal consumption estimates (Fig. 2). Many of the estimates of salmonid consumption had exceedingly poor precision with the coefficient of variation exceeding 0.5 (Table 3). Using adult chinook salmon (*O. tshawytscha*) as an example, an examination of the variance components demonstrated that estimation of biomass (Table 4) was the predominant source of variance. Variance associated with biomass estimation includes variation in predicted weights and estimation of number of prey (\hat{n}_i) for salmonids. The latter accounted for one- to two-thirds of the total variance for salmonids depending on the species and size group. The use of genetics to obtain species identification of the unknown salmonids identified by bone would substantially improve the precision for salmonids.

Using BR to estimate diet composition, adult chinook salmon was the only salmonid that was consistently in the five most important prey items for each season based on percent of biomass (Fig. 1). Their importance was derived from their average mass which was the largest of all the prey. Adult chinook salmon and the other salmonids appeared much less important if the ranking was based on the number consumed (Fig. 2). Smaller prey items such as herring (*Clupeid spp.*), sculpin (*Leptocottus armatus*), lamprey (*Petromyzontid spp.*), smelt (*Osmeridae*) and

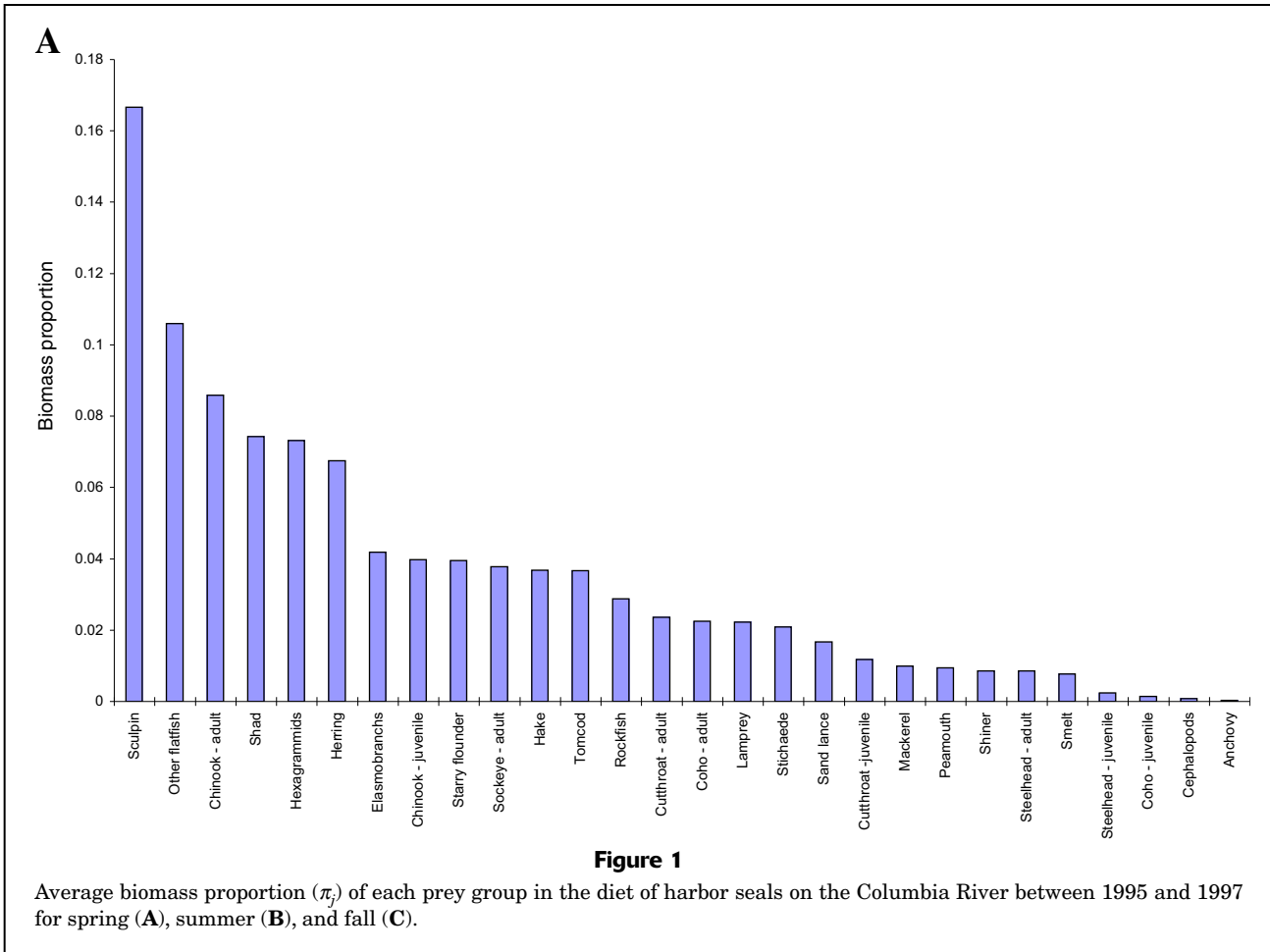
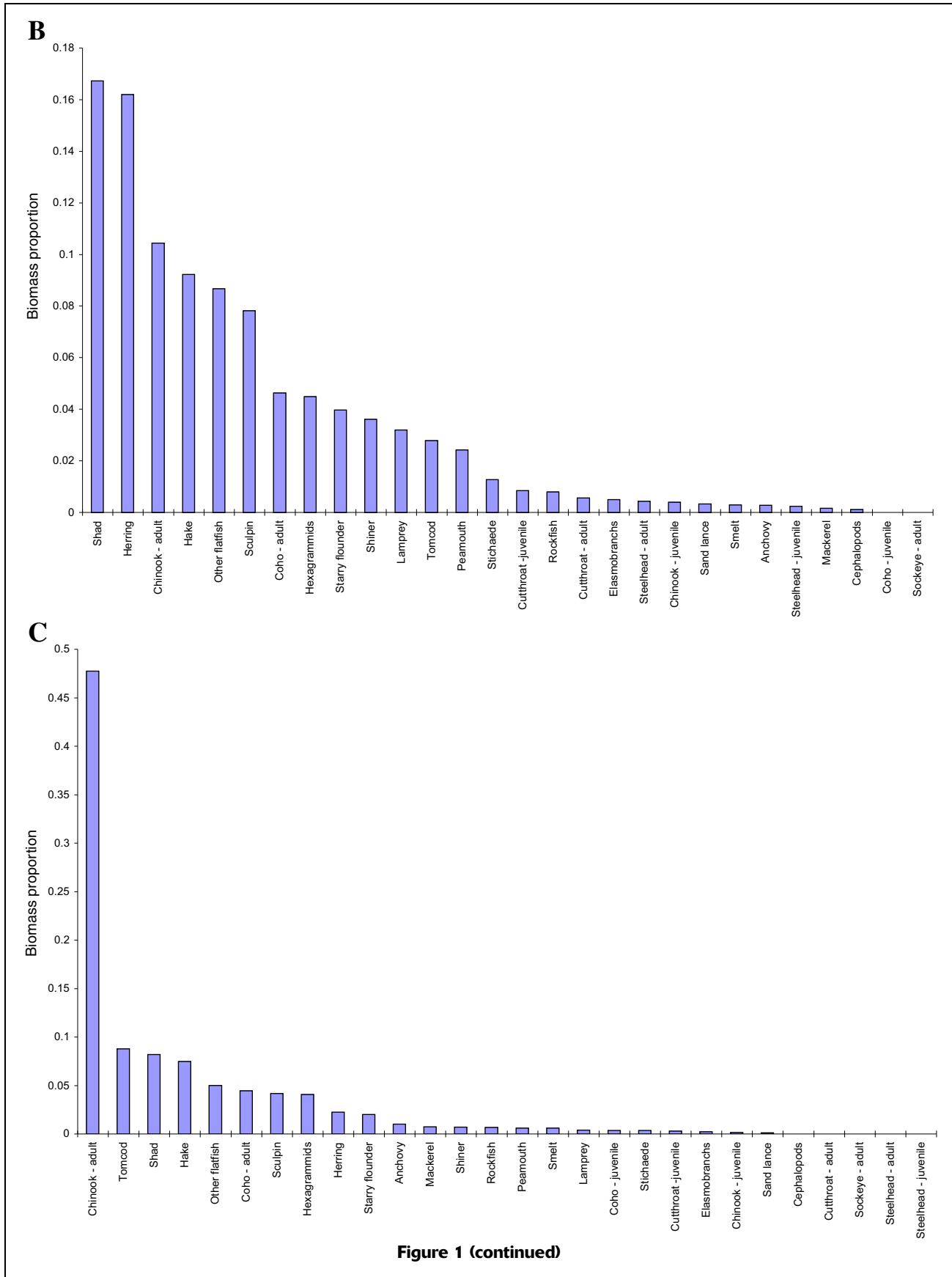


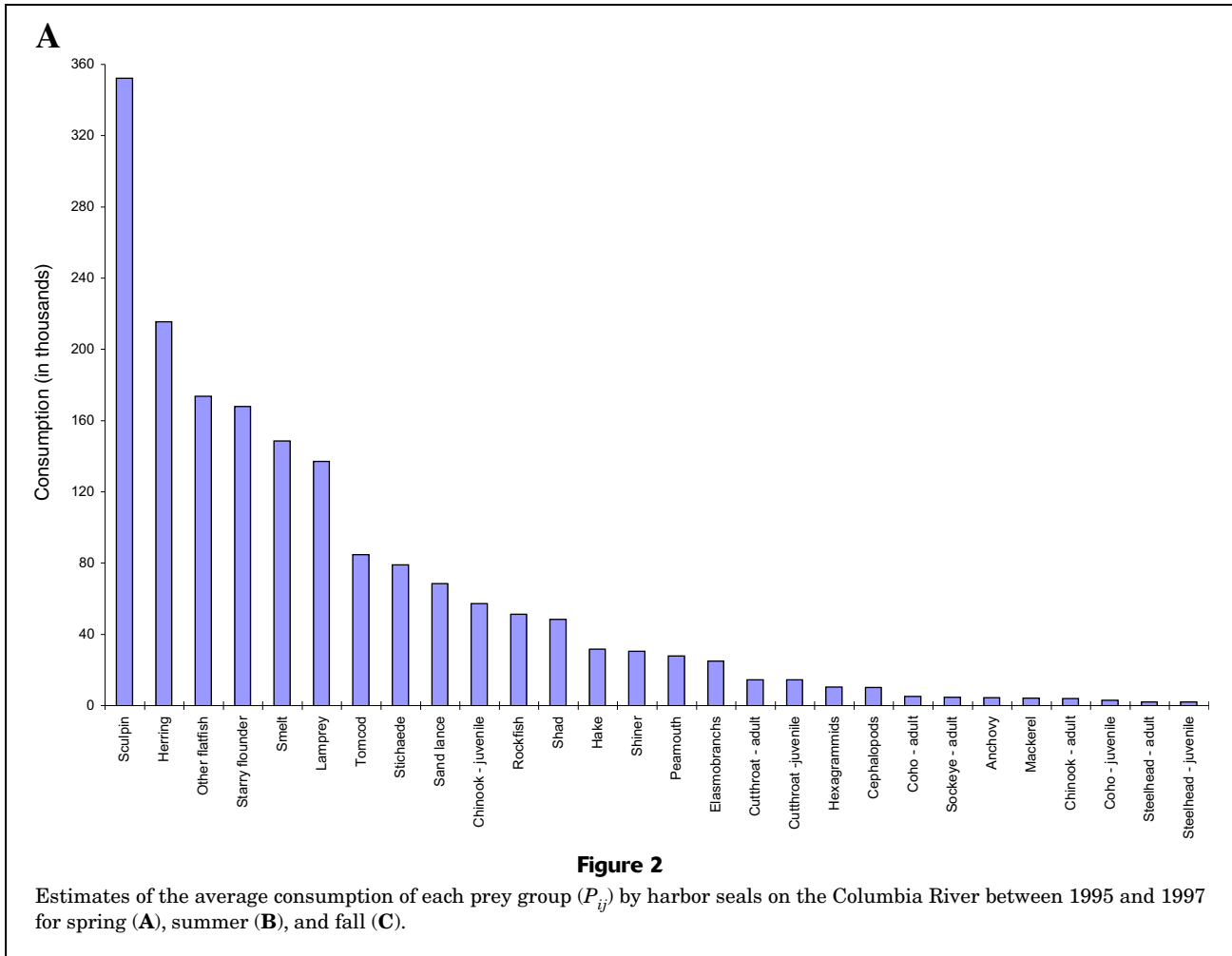
Table 3
Average seasonal estimates of the number of salmonids consumed by harbor seals during 1995–97 (P_i) (in 1000s) and its coefficient of variation (CV) based on the biomass reconstruction (BR) method for diet composition.

Species	Size	Spring		Summer		Fall	
		P_i	CV	P_i	CV	P_i	CV
Chinook (<i>O. tshawytscha</i>)	Adult	3.9	0.65	3.1	0.44	15.6	0.30
	Juvenile	57.1	0.39	18.0	0.32	2.4	1.11
Coho (<i>O. kisutch</i>)	Adult	5.1	0.73	13.3	0.32	7.3	0.65
	Juvenile	2.8	0.85	0.0	0.00	4.9	0.76
Cutthroat (<i>O. clarkii</i>)	Adult	14.2	0.40	2.2	0.42	0.0	0.00
	Juvenile	14.2	0.40	6.6	0.38	2.3	1.08
Sockeye (<i>O. nerka</i>)	Adult	4.4	0.45	0.0	0.00	0.0	0.00
Steelhead (<i>O. mykiss</i>)	Adult	2.0	0.99	0.6	0.64	0.0	0.00
	Juvenile	2.0	1.00	1.3	0.57	0.0	0.00

anchovy (*Engraulis mordax*) were consumed in greater quantity but they were not always a large proportion of the reconstructed biomass.

Using split-sample frequency of occurrence (SSFO) to estimate diet composition, the results were dramatically different for larger and smaller prey items (Fig. 3). For





prey items weighing 10–20 g, SSFO predicted consumption that was 10 times greater than BR. Likewise, for prey items with a 1 kg mass or greater, SSFO predicted consumption estimates that were less than one-tenth of the BR estimate. For prey items near the median mass of 173 g, both estimators produced similar results.

Discussion

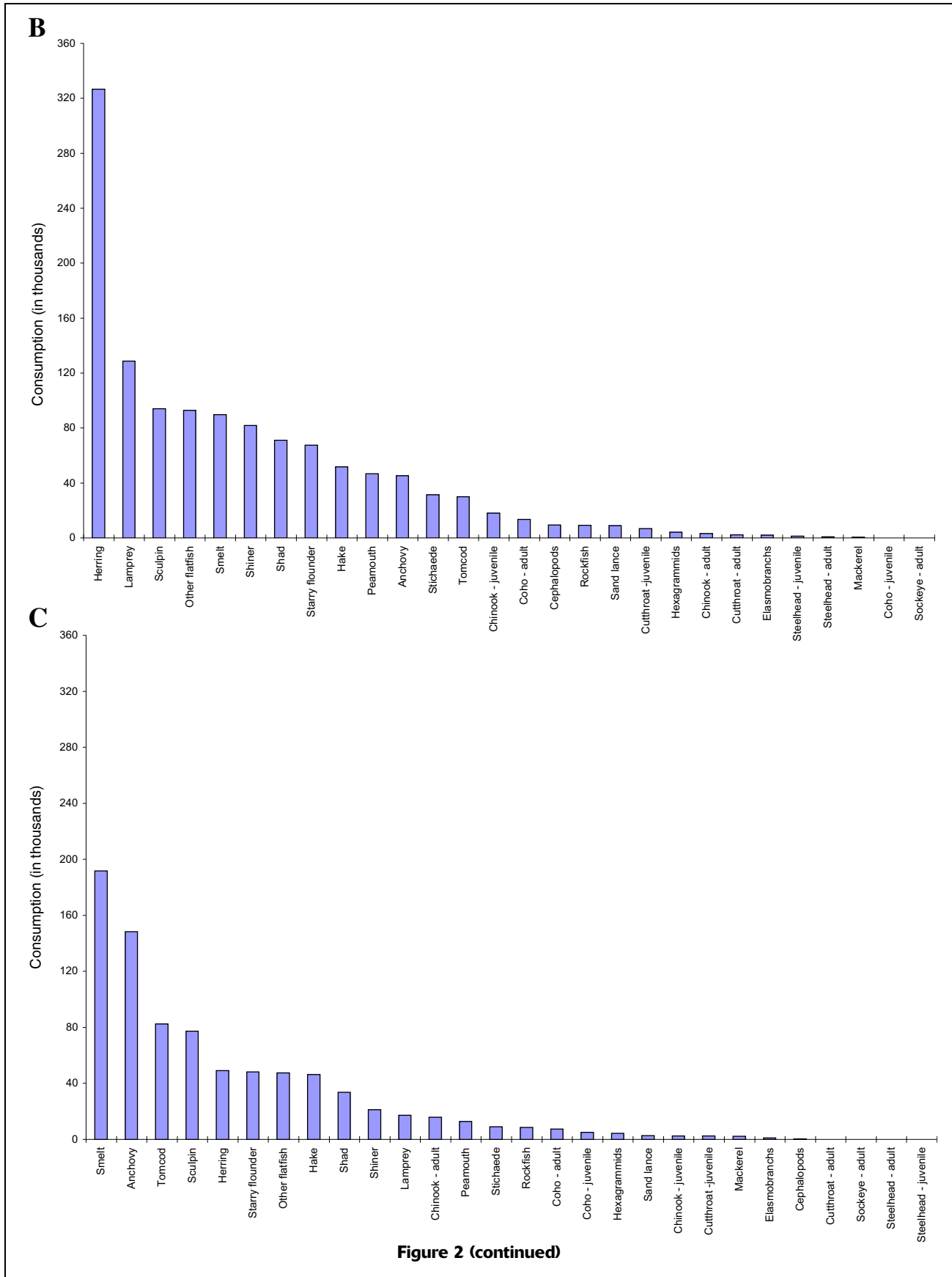
The consumption estimates for the Columbia River harbor seals could be improved by incorporating differences in energy density across prey and by measuring the sex- and age-structure of the seal population through time rather than using a life-table which may not be appropriate. These are valid criticisms and they could be overcome by collecting additional data. However, we believe these are less important than the current inadequacies in measuring diet composition that will likely affect any study that attempts to estimate consumption based on scat analysis.

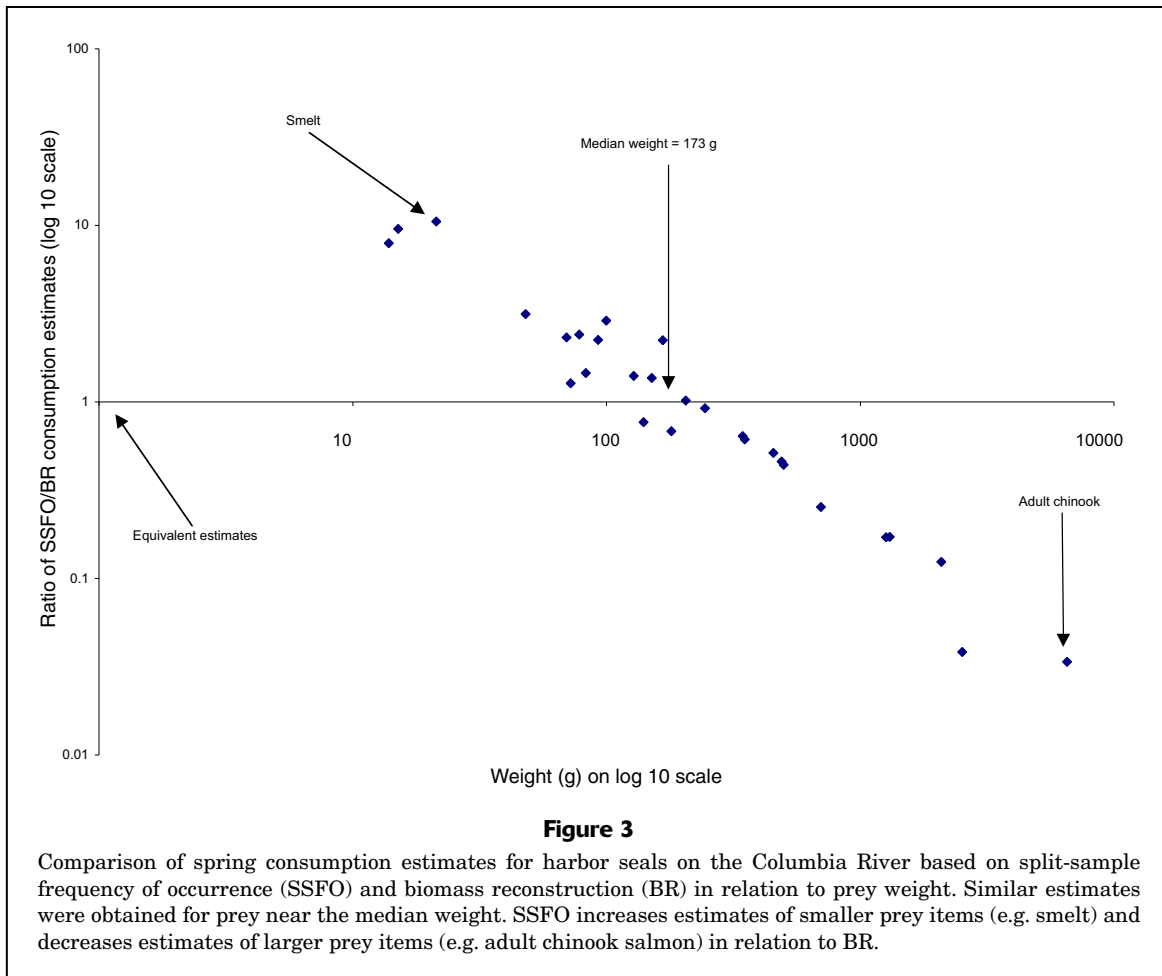
It is well recognized that digestion does not act equally on all hard parts and is certainly species-specific for otoliths (Harvey, 1989). We included other hard parts such

Table 4
 Proportion of variance of the adult chinook consumption estimate resulting from each estimation component.

Season	Diet composition		Harbor seal	
	Year (σ_y)	Date (σ_t)	Biomass (σ_r)	Population size
Spring	0.00	0.14	0.82	0.04
Summer	0.00	0.51	0.44	0.04
Fall	0.20	0.16	0.59	0.05

as bone to reduce bias due to differential otolith digestion; however, that inclusion may not remove all of the selectivity bias and it certainly introduces several other problems discussed below. Also, because hard parts are used for diet composition, if seals are only eating the fleshy parts of large fish, a significant portion of their diet may be missed.





We have assumed an equal probability of recovering identifiable skeletal remains from all prey sizes and that masses predicted from otolith measurements represent prey identified from other structures. There are several situations when recovered otoliths may not correctly represent the size of prey consumed. Small otoliths from small individuals of a species may be more likely to be completely digested. In that case, biomass would be overestimated because the larger otoliths would be recovered from larger fish. Also, otoliths may have different passage rates due to changes in their structure as fish age resulting in a size bias. Consumption estimates could thus be erroneously high or low because prey would be calculated from a single size group rather than the range of prey consumed. Unequal digestion may also create errors in estimated mass from the otoliths that are recovered. Our estimated mass may have been biased because we applied an average degradation factor to adjust otolith length. A better alternative would be to grade otolith condition and apply condition-specific degradation factors (Tollit et al., 1997b).

Counting the number of individual prey items is not possible with nonunique bones. Instead, we estimated a minimum number of individuals (MNI) contained in the

scat (n_{ij} =MNI). MNI from all skeletal elements is a minimum estimate because the presence of many nonunique structures are assigned to a single prey item when they could represent several different prey. This error would not bias diet composition if it did not vary over species and size. However, differential passage of unique structures and identifiability among species result in the greater probability of detecting some prey (Browne et al., 2002). To minimize interspecific biases, we could use an MNI of 1 for all bones, regardless of the enumeration of unique structures for some species. While this would reduce some problems with species differences, it would exacerbate differences associated with prey size because large prey would be accurately reflected by an MNI of 1 and small prey that are eaten in greater quantities would be severely underestimated.

Bowen (2000) proposed estimating the number of prey consumed by correcting the otolith count with rates of otolith recovery from feeding trials. These correction factors vary widely between seals and studies and are influenced by a variety of factors, including size of individual prey, meal size, and activity of harbor seals (Harvey, 1989; Harvey and Antonelis, 1994; Cottrell et al., 1996; Tollit et al., 1997b). Browne et al. (2002) examined the ratio of otolith-

corrected estimates of MNI for several species. The ratios were quite variable but the comparison did suggest that smaller prey such as smelt were more likely to be under-represented by using the minimum count.

If diet composition is based on sagittal otoliths, a fish can be represented by, at most, two scats and because all fish have two sagittal otoliths, fish size should not influence the probability that a particular fish is included, in a sample of scats, except through size-specific passage rates of otoliths. However, when all hard parts are included, the sampling may be size-biased if the size of the prey affects the number of scats in which the hard parts are deposited. Larger prey contain larger hard parts that may require longer passage times; therefore larger prey may be deposited in more scats than smaller prey. Also, large prey may be shared among seals as a result of cooperative feeding behavior and could be deposited in several scats. If either situation occurs, larger prey would be more likely to be included in the sample and would be over-represented. Because the scat is the sampling unit, any prey-size or species-specific effects on scat deposition rate may also bias diet composition estimators.

The effect of over-representing large prey depends on the estimator used for diet composition. The different outcomes with Equations 1–3 can be demonstrated with a simple example. Consider a sample of two scats in which one scat contains the remains of a 2-kg salmon and another scat contains the remains of ten 10-g anchovy and four 100-g herring. From Equation 1, the diet composition would be 80% (2000/2500) salmon, 4% anchovy, and 16% herring based on proportions of total reconstructed biomass. From Equation 2, we would estimate that salmon represent 50% of the diet from the two samples that are 100% and 0% salmon, and likewise 10% anchovy and 40% herring. Finally from Equation 3, we would estimate that the diet was 50% salmon, 25% anchovy, and 25% herring. If the small prey were undercounted in relation to the large salmon, the influence of the error influences the composition within the scat for Equations 2 and 3, but for BR (Eq. 1) the error extends across all samples.

As with the Columbia River harbor seal example (Fig. 3), the differences in the estimators are primarily the result of large prey in the weighted versus unweighted averages. Some difference would be expected in the results of Equations 2 and 3 depending on the validity of the equal volume assumption. SSFO (Eq. 3) simplifies the analysis of diet composition to a measure of presence and absence by assuming that prey within the same scat were consumed in equal volumes. The simplifying assumption removes the necessity to enumerate prey and measure mass from morphometric relationships with prey remains. However, the equal volume assumption does not seem particularly reasonable and its implementation is arbitrary, depending on how the prey are classified unless all prey remains can be identified to species. Olesiuk (1993) showed that the diet composition percentages for the primary prey varied by a factor of two or three, depending on the assumed composition within each scat. We expected that these differences would depend on the diversity of the diet. How closely they represented the true diet would depend on the range in prey sizes.

From our viewpoint, we do not see a clear choice between the estimators for diet composition. The use of consumption estimates from SSFO and BR to provide a range of estimates may have limited application in cases where each approach would suggest a similar conclusion. However, for large prey, such as salmonids, a tenfold difference in estimates, compounded with the uncertainty from sampling and biomass estimation, may yield too little information to develop a reliable conclusion about the impact of pinniped predation on salmonid stocks.

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Appendix

We have constructed variance estimators for diet composition and consumption rates using finite population sampling methods (Cochran, 1977) and delta method approximations based on the Taylor series (Seber, 1973). Variance estimates and confidence intervals could also be constructed by using bootstrap techniques similar to the work of Hammond and Rothery (1996).

To describe the variance estimators, we use the following subscripts: i for prey group, j for season, y for year, and t for collection occasion within year. A dropped subscript implies summation or averaging over that subscript (e.g. s_{jy} is the total number of scats collected in season j of year y —summed over occasions). We define the following notation which was not used in our article:

T_{jy} = number of scat collection occasions,
 s_{jy} = number of scats collected during the occasion,
 Y_j = number of years in which season j was sampled of a total of Y years.

We have assumed that scat collected on each occasion is a varying proportion of a fixed and unspecified amount of prey biomass consumed. Thus, we computed unweighted averages of the proportions over occasions and then over years:

$$\hat{\pi}_{ijy} = \frac{\sum_{t=1}^{T_{jy}} \hat{\pi}_{ijyt}}{T_{jy}} \quad \hat{\pi}_{ij} = \frac{\sum_{y=1}^{Y_j} \hat{\pi}_{ijy}}{Y_j}.$$

We have also assumed that scat samples are independent which would be a concern in the unlikely event that the same seal deposited multiple scats at one time. We have also assumed that the collection occasions which are limited to low tides represent a random sample of dates within a season.

The variance of diet composition was based on multistage sampling scheme stratified by season (Cochran, 1977) that was composed of the following stages: estimation of biomass proportion consumed for each occasion, sampling of occasions within season of a year, and sampling of years. We have limited inference to the Y years that were sampled. Thus, if a season was sampled in each

year there is no annual variance component. The variance of the diet composition for a prey group for a single season is the sum of three components corresponding to the three stages: estimation of biomass proportion (σ_b^2), sampling of occasions (σ_t^2), and sampling of years (σ_y^2). Following Cochran (1977), the estimators for each component are

$$\hat{\sigma}_b^2 = \frac{\sum_{y=1}^{Y_j} \sum_{t=1}^{T_{jy}} \widehat{Var}_b(\hat{\pi}_{ijyt})}{\sum_{y=1}^{Y_j} T_{jy}},$$

$$\hat{\sigma}_t^2 = \frac{Y_j}{Y} \frac{\sum_{y=1}^{Y_j} \sum_{t=1}^{T_{jy}} (\hat{\pi}_{ijyt} - \hat{\pi}_{ijy})^2}{\sum_{y=1}^{Y_j} T_{jy} \sum_{y=1}^{Y_j} (T_{yj} - 1)},$$

$$\hat{\sigma}_y^2 = \frac{\left(1 - \frac{Y_j}{Y}\right) \sum_{y=1}^{Y_j} (\hat{\pi}_{ijy} - \hat{\pi}_{ij})^2}{Y_j(Y_j - 1)}.$$

We used the delta-method (Taylor series approximation) (Seber 1973) to estimate the variance of the estimated proportion for occasion t which expressed in matrix notation is

$$\widehat{Var}_b(\hat{\pi}_{ijyt}) = \widehat{Var}_b \left(\frac{\hat{b}_{ijyt}}{\sum_{r=1}^{\omega} \hat{b}_{rjyt}} \right) = \beta' \Sigma \beta,$$

where β is a vector of partial-derivatives of π_{ijyt} with respect to b_{rjyt} for $r=1, \omega$ and Σ is the $\omega \times \omega$ variance-covariance matrix of \hat{b}_{rjyt} for $r=1, \omega$. Likewise, the variance of ρ_{ij} was estimated by using

$$\widehat{Var}(\hat{\rho}_{ij}) = \left[\frac{\hat{\sigma}_y}{\bar{w}_{ij}} \right]^2 + \left[\frac{\hat{\sigma}_t}{\bar{w}_{ij}} \right]^2 + \hat{\sigma}_\rho^2,$$

where

$$\hat{\sigma}_\rho^2 = \frac{\sum_{y=1}^{Y_j} \sum_{t=1}^{T_{jy}} \widehat{Var}_b(\hat{\rho}_{ijyt})}{\sum_{y=1}^{Y_j} T_{jy}},$$

and
$$\widehat{Var}_b(\hat{\rho}_{ijyt}) = \widehat{Var}_b \left(\frac{\hat{n}_{ijyt}}{\sum_{r=1}^{\omega} \hat{b}_{rjyt}} \right) \approx \beta' \Sigma \beta,$$

where the elements in Σ and β for the i^{th} prey group are partitioned into \hat{n}_{ijyt} and \bar{w}_{ij} . We also used the delta-method to obtain approximate variances and covariances in Σ of the biomass estimates for a single occasion

$$\widehat{Var}(\hat{b}_{ijyt}) = \hat{n}_{ijyt}^2 \hat{\sigma}_w^2 + \hat{\sigma}_n^2 \bar{w}_{ij}^2.$$

The first term in the variance is the uncertainty resulting from the variability in the estimate of the mean weight. For salmonid species, the second term measures the uncertainty resulting from apportioning the number of unknown salmonids into prey groups (i.e. estimating n_{ijyt}). For nonsalmonid species, all hard parts were classified into less specific prey groups; therefore $\hat{\sigma}_n = 0$. The group-specific estimates of biomass within season are uncorrelated except for the estimates for salmonid species ($i \in \Psi$) which are correlated because of the apportionment of the items which were identified as salmonid but could not be identified to species nor to the juvenile and adult sizes. For salmonid groups r and $v \in \Psi$, the estimated covariance is

$$\widehat{Cov}(\hat{b}_{rjyt}, \hat{b}_{vjyt}) = \widehat{Cov}(\hat{n}_{rjyt}, \hat{n}_{vjyt}) \bar{w}_{rj} \bar{w}_{vj}.$$

The total amount of biomass represented by the scats is the sum across all prey groups:

$$\hat{b}_{jyt} = \sum_{i=1}^{\omega} \hat{b}_{ijyt},$$

and its variance was estimated as

$$\widehat{Var}(\hat{b}_{jyt}) = \sum_{i=1}^{\omega} \widehat{var}(\hat{b}_{ijyt}) + 2 \sum_{r \in \Psi} \sum_{v > r; v \in \Psi} \widehat{cov}(\hat{b}_{rjyt}, \hat{b}_{vjyt}).$$

The variance of n_{ijyt} was estimated assuming a binomial distribution:

$$\widehat{Var}(\hat{n}_{ijyt}) = \sigma_n^2 = u_{jyt}^2 \frac{\hat{\gamma}_{ij}(1 - \hat{\gamma}_{ij})}{o_{ij}},$$

and the covariance between salmonid groups was estimated as

$$\widehat{Cov}(\hat{n}_{rjyt}, \hat{n}_{vjyt}) = -u_{jyt}^2 \frac{\hat{\gamma}_{rj} \hat{\gamma}_{vj}}{o_{ij}}.$$

We assumed that the weights of the prey consumed were independent samples from a group- and season-specific distribution with mean μ_{ij} and variance σ_{ij}^2 . The parameters μ_{ij} and σ_{ij}^2 were estimated with the predicted weights from the sample of o_{ij}^* measurable hard parts:

$$\hat{\mu}_{ij} = \bar{w}_{ij} = \frac{\sum_{u=1}^{o_{ij}^*} \hat{w}_{iju}}{o_{ij}^*} \quad \text{and} \quad \hat{\sigma}_{ij}^2 = \frac{\sum_{u=1}^{o_{ij}^*} (\hat{w}_{iju} - \bar{w}_{ij})^2}{o_{ij}^* - 1}.$$

To incorporate uncertainty in regression parameters and prediction error for the measured hard parts and variability in mass for the unmeasured prey ($n_{ij} - o_{ij}^*$), the variance of μ_{ij} should be estimated by

$$\widehat{\text{Var}}(\bar{w}_{ij}) = \hat{\sigma}_w^2 = \frac{\sum_{u=1}^{o_{ij}^*} \widehat{\text{Var}}(\hat{w}_{iju})}{o_{ij}^{*2}} + \left(\frac{n_{ij} - o_{ij}^*}{n_{ij}} \right) \frac{\hat{\sigma}_{ij}^2}{o_{ij}^*},$$

where the variance of \hat{w}_{iju} is the prediction variance for the u^{th} otolith. When these data were analyzed, the available regression equations in a draft version of Harvey et al. (2000) did not include standard errors for the parameters nor the residual variance that were needed to compute the prediction variance. Therefore, unfortunately we had to drop the first term from the variance. The necessary values are now available in Harvey et al. (2000). The second-term measures variability between prey and is typically larger than the prediction error. However, to avoid underestimating this component of variance we dropped the finite popu-

lation correction (fpc) factor on the second term. If we had used the fpc for salmonids, we would have had to replace the unknown n_{ij} with their estimated values.

For variance estimates of number of prey consumed (P_{ij}) we also used a delta method approximation:

$$\widehat{\text{Var}}(\hat{P}_{ij}) \approx \hat{P}_{ij}^2 [cv^2(\xi_j) + cv^2(\hat{\rho}_{ij})].$$

We did not have variance estimates for energetic requirements nor age structure; therefore the variation in estimated prey biomass requirement (ξ_j) reflected only variation in our estimates of population size:

$$cv(\xi_j) = cv(\hat{N}_j) \approx \sqrt{cv^2(\bar{c}_j) + cv^2(f)},$$

which was also approximated by the delta method.