Assessing the use of hard parts in faeces to identify harbour seal prey: results of captive-feeding trials

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Abstract: Faeces were collected from four captive harbour seals (*Phoca vitulina*) that consumed known amounts of herring (*Clupea harengus*), walleye pollock (*Theragra chalcogramma*), Pacific hake (*Merluccius productus),* surf smelt *(Hypomesus pretiosus),* and juvenile chinook salmon *(Oncorhynchus tshawytscha*). The goal was to determine which structures (hard parts) passed through the digestive tract (e.g., eye lenses, scales, vertebrae, otoliths), and which of these could be used to determine the type and number of fish consumed. Nearly 5000 fish were consumed, from which over 50000 hard parts were recovered from seal faeces. Scales were the most numerous of the 23 structures recovered (> 20 000), followed by vertebrae, eye lenses, and otoliths. Morphological distinctiveness and digestive erosion of the structures varied among fish taxa. Two to five structures accounted for over 90% of the taxon-specific elements recovered, depending upon the species of fish consumed. Otoliths, which are used routinely to characterize pinniped diets, accounted for only 17% of the identified taxon-specific hard parts. The variation in types of structures and rates of recovery across taxa underscores the importance of using several types of hard parts to identify prey. Identifying several different prey structures increases the likelihood of identifying a prey type.

Résumé : Les feces de quatre Phoques communs (*Phoca vitulina)* gardés en captivité et nourris de quantitts connues de Hareng atlantique (*Clupea harengus*), de Goberge de l'Alaska (*Theragra chalcogramma*), de Merlu du Pacifique *(Merluccius productus),* d'Éperlan argenté *(Hypomesus pretiosus)* et de Saumon quinnat *(Oncorhynchus tshuwytschu)* juvenile, ont été examinées. Le but de l'opération Ctiat de nous aider à reconnaitre quelles structures non digérées (parties dures, e.g., cristallins, Ccailles, vertèbres, otolithes) peuvent servir à determiner le type et le nombre de poissons consommés. Près de 5000 poissons ont été consommés et 50000 parties dures ont été récupérées dans les feces. Les écailles Ctaient les structures les plus nombreuses des 23 structures récupérées (> 20 000), suivies des vertèbres, cristallins et otolithes. Les particularités morphologiques et l'érosion des structures après la digestion différaient d'une espèce de poisson à l'autre. De deux à cinq structures constituaient plus de 90% des elements spécifiques à chaque taxon, et ce nombre variait selon l'espèce de poisson consommée. Les otolithes, qui servent couramment dans l'étude des regimes alimentaires des pinnipèdes, ne constituaient que 17% des parties dures identifiées de taxons particuliers. La variation d'un taxon à l'autre des types de structures et de leur taux de recuperation dans les feces souligne l'importance d'utiliser divers types de structures dures pour identifier les proies. L'identification d'un nombre élevé de structures augmente la probabilité d'identifier correctement le type de proie.
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Introduction

The prey consumed by pinnipeds are usually identified from the teleost otoliths and cephalopod beaks that resist digestion found in pinniped stomachs and faeces (e.g., Scheffer and Slipp 1944; Fisher 1952; Spalding 1964; Rae 1973; Pitcher 1980*a*, 19806; Roffe and Mate 1984; Perez and Bigg 1986; Prime and Hammond 1987; Murie and Lavigne 1991). However, some prey may not be identified as part of a seal's diet because of partial or complete digestion of otoliths in the gastrointestinal tract (Prime 1979; da Silva and Neilson 1985; Murie and Lavigne 1986; Jobling 1987; Murie 1987; Dellinger and Trillmich 1988; Harvey and Antonelis 1994). Similarly, prey species that lack identifiable otoliths (e.g., cartilaginous fishes) or whose otoliths are not ingested are not represented in digestive tracts or faeces (Scheffer and Slipp 1944; Spalding 1964; Boulva and McLaren 1979; Pitcher 1980b; Roffe 1981; Cottrell 1995). Factors such as these, that bias the recovery of otoliths, have led some investigators to question the reliability of diet estimates based on otoliths (Jobling and Breiby 1986; Jobling 1987).

Although many hard parts other than otoliths and beaks are found in stomach and faecal remains (Fitch and Brownell 1968; Pitcher 1980b; Bigg and Fawcett 1985; Prime and Hammond 1990; Croxall 1993; Cottrell 1995), it is only recently that they are being used to identify prey. For example, Roffe and Mate (1984) identified Pacific lamprey (*Lampetra*

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Table 1. Harbour seals used in feeding trials.

Seal	Sex	Age (yr)	Mean mass during trials (kg)
Aretha	F	> 12	93
Dolly	F	10	80
Benny	M	5	85
Morgan	M	3	65

tridentata) by means of infraoral and supraoral structures found in harbour seal and California sea lion *(Zalophus californianus*) digestive tracts. Similarly, Olesiuk et al. *(1990)* and Cottrell *(1995)* identified 58 and 55% of fish prey, respectively, using hard parts other than otoliths recovered from harbour seal *(Phoca vitulina)* faeces.

Captive-feeding studies are one means of understanding and correcting the biases in the number, size, and type of prey recovered from faeces. Past studies on captive pinnipeds have estimated recovery rates of otoliths (da Silva and Neilson 1985; Murie and Lavigne 1985; Dellinger and Trillmich 1988; Harvey 1989; Harvey and Antonelis 1994). However, none have extended this approach to other fish structures, nor has cross-validation between otoliths and other hard parts been carried out.

The present study was designed to meet some of these shortcomings. The main objectives were to (i) determine which taxon-specific hard parts pass through the harbour seal digestive tract, (ii) identify which taxon-specific structures are useful for qualitative and quantitative estimates of fish consumed, and *(iii)* compare the accuracy of identifying prey using otoliths and other hard parts.

Methods

Recovery of fish hard parts

Four captive harbour seals (two males and two females) were housed individually in continuously flowing salt-water tanks (5 x 2 x 2 m) at the Vancouver Aquarium (Table 1). The animals had access to a 1 x 2 m haulout platform and were fed twice per day. They consumed 5 – 8 % of their body mass each day in 5- to 15-day experiments from January to June 1993. Five species of fish were used: Pacific herring (*Clupea harengus pallasii*), walleye pollock (*Theragra chalcogramma*), Pacific hake (*Merluccius productus),* surf smelt (*Hypomesus pretiosus),* and juvenile chinook salmon *(Oncorhynchus tshawytscha*)

Standard lengths and masses of all fish were recorded to 5 mm and 0.1 g accuracy, respectively (Table 2). Each day seals were fed with one of five prey types, with the sequence repeated after 5 days. Initial feeding trials indicated that the seals tore the heads off fish that were too large to be swallowed whole. Nondigested otoliths of these large prey were found 1 h after the seals were fed, when the tank was cleaned. No other structures[3] from these prey items were recovered during tank cleaning. However, digested structures from these prey items were recovered during the next tank cleaning (i.e., 24 h later). The minimum passage rate of food in captive pinnipeds is believed to be 6 h (Prime 1979). Thus, the otoliths from the large food items recovered after 1 h were assumed to have fallen out of the cranial cavity during ingestion. Subsequently, only fish that could be swallowed whole were fed to seals in this experiment.

[3] "Structure" indicates the hard part types and "element" refers to their frequency, e.g., 3 gill rakers plus 2 otoliths equals 2 structures but 5 elements.

Table 2. Sizes and numbers of fish fed to harbour seals.

	Length (mm)	Mass (g)	N
Herring	183 ± 16.6	121 ± 17.7	1978
Hake	331 ± 18.3	344 ± 56.9	145
Pollock	293-f-32.1	372 ± 118.2	119
Salmon	143 ± 8.3	51 ± 10.2	74
Smelt	167 ± 11.7	49 ± 14.5	1530

Note: Values are given as means ± SD.

Tanks were drained and cleaned daily by filtering their contents through 0.495-mm nylon mesh fitted to the outflow. Hard parts from faecal material were dried and stored in petri dishes until examination.

Fish structure recovery test

The ability to successfully recover fish hard parts was tested by scattering 20-25 marked vertebrae, otoliths, or postcleithra from herring, pollock, and salmon into the tank. All marked elements were recovered during the next tank cleaning. Thus, we assumed that all fish hard parts passed in faeces during each trial were recovered.

Identification of prey hard parts

Fish hard parts recovered from the scats were compared with a voucher collection held at the Department of Anthropology, University of Victoria. Fish scales were identified by staff at the Pacific Biological Station (Nanaimo, B.C.). Hard parts were identified to the lowest possible taxon using a dissecting microscope (8-24 x). Naming of hard parts followed Casteel (1976) and Cannon (1987).

Some structures recovered from the faecal remains were not morphologically distinct enough to be of use in identifying prey. Structures diagnostic of taxa were chosen for statistical analysis and separated into three categories. (1) Type and number: structures that could be used to estimate the number of prey consumed, and that represented > 10% of the prey species fed (e.g., otolith, atlas-axis, and postcleithrum); structures that accounted for < 10% of the fish consumed would be of little use for quantitative estimates. (2) Type only: structures that represented < 10% of the total fish eaten or were not suitable for estimating the number of a particular species consumed (i.e., structures that have numerous elements that often vary within taxa) but could be used to determine the presence or absence of a prey taxon (e.g., scale, tooth, and vertebra other than the atlas or axis). (3) Number only: structures that could not be used to identify prey but whose frequency could be used to estimate the number of fish eaten (e.g., eye lens).

Estimates of the proportion of prey consumed were computed as the greatest number of left or right category 1 elements (nonpaired structures were simply counted) divided by the total number of fish fed to the seal during the experiment. In some cases the estimate was based on the total number of elements recovered divided by 2, when erosion or fragmentation made determining right or left side impossible. Category 2 and 3 structures were simply counted.

Recovery rates (as proportions) of category 1 structures were arcsine-transformed for statistical analysis (Zar 1984). Analysis of variance (ANOVA) was used to test whether differences in rates of recovery of fish structures among seals were statistically significant.

Results

Over 50 000 elements were recovered from the 4946 fish fed to the four seals during the 6-month experimental period.

Table 3. Results of ANOVAs on recovery rates (%) of fish structures for different seals.

	Structure(s)	df	F	P
Herring	Otolith	3,8	2.96	>0.05
	Prootic-synotic	3,8	3.54	>0.05
	Atlas-axis	3,8	11.7	>0.05
Hake	Otolith	2,4	0.66	>0.05
Pollock	Otolith	2,6	0.92	>0.05
	Postcleithrum	2,6	1.00	>0.05
	Interopercle	2,6	0.60	>0.05
Salmon	Otolith	3,8	16.00	<0.05
Smelt	Otolith	2,7	0.63	<0.05

Of these elements, 22 383 (22 structures) were diagnostic of taxa (categories 1 and 2). In addition, 7963 lenses were recovered (category 3).

Differences in recovery rates of 8 of the 9 structures did not differ significantly among the four seals (Table 3), but there was a significant difference in the recovery rate of salmon otoliths. A Tukey's test ($F_{[3,8]} = 7.93$, $P = 0.05$) revealed that for seal 4 (the youngest animal), the recovery rate of salmon otoliths was unusually low. In general, it appears that structure recovery rates among seals were not significantly different. Thus, we pooled the results of individual feeding trials.

Otoliths were the only category 1 structures that were useful for estimating the number of fish consumed for all species. Overall, between 23 and 77% of all otoliths were recovered ($\bar{x} = 54\%$), but recovery rates differed significantly among fish species ($F_{4,39} = 5.39$, $P < 0.05$). Otoliths were the only structure recovered that were useful for estimating the numbers of smelt and salmon consumed. However, additional structures recovered from herring (atlas-axis, prootic −synotic), pollock (postcleithrum, interopercle, dentary), and hake (dentary) were useful for making quantitative estimates (Table 4). The atlas and axis and prootic and synotic were combined for herring because the erosion of characteristics distinguishing the groups made separate structure identifications unreliable. Interestingly, the recovery of herring atlas and axis structures provided a 5 % improvement over otolith estimates for the number of herring consumed. Similarly, herring prootic and synotic bones provided a 2% higher estimate.

The most abundant hard part recovered was scales. In a small sample, 23 of 30 scales (77%) were identified to species (9 scales), genus (6), or family (8). In addition, age could be estimated from 12 of the scales (40%).

The second most abundant structure recovered was vertebrae (14 853; including the axis, atlas, and other vertebrae that were taxon-specific). Vertebrae made up > 66 % of the taxon-specific hard parts identified. Some fish taxa have distinctive vertebrae that are diagnostic of species (e.g., herring, hake). Other vertebrae can be identified to genus (e.g., salmon, smelt) or family (e.g., pollock). The diagnostic properties of structures varied among taxa (Table 5). Many other fish hard parts were also present and potentially diagnostic of taxa. However, the huge effort to sort, enumerate, and catalogue the small number of elements recovered from the remaining structures would have contributed little to overall prey identification. Nevertheless, as techniques for identifying fish hard parts improve, some of these additional structures may prove useful for prey identification.

Table 4. Fish structures that could be used to detect the incidence or presence (+) of prey species.

Structure(s)	Herring	Hake	Pollock	Salmon	Smelt
Vertebra	+	+	+	+	
Otolith	**29.8**	72.8	76.5	62.4	23.1
Prootic−synotic	**32.5**	–	–	–	
Atlas -axis*	**35.3**	–	–	+	
Dentary	+	35.5	35.3	+	
Gill raker	–	+	+	+	
Tooth	–	+	–	+	
Ultimate vertebra	+	–	–	–	
Postcleithrum	–	–	55.9	–	
Ceratohyal	+	–	–	–	
Epihyal	+	+	–	–	
Interopercle	–	–	28.7	–	
Pharyngobranchial	–	+	+	+	
Angular	–	+	+	–	
Quadrate	+	–	–	–	
Hypobranchial	–	+	+	–	
Epibranchial	–	–	+	–	
Basioccipital	+	–	–	–	
Hyomandibular	+	–	–	–	
Scale	+	–	–	+	

Note: For category 1 structures, percent recovery is indicated (see the text).
*Identifications of herring include the atlas and axis, otherwise only the atlas.

We found that 2 -5 category 1 and 2 structures per fish taxon represented > 90% of all elements recovered. The average number of structures recovered per fish (excluding scales) ranged among species from 0.98 to 4.28. Numbers of elements ranged from 1.08 to 7.27 (Table 6).

The category 3 structure, the eye lens, provided the best estimate of the numbers of fish consumed. In all, 7963 eye lenses were recovered, representing 80.5 % of the fish eaten. Unfortunately, it is presently not possible to identify prey species from eye lenses.

Discussion

Feeding studies on captive seals are currently the best way to evaluate the accuracy of estimating pinniped diets from prey hard parts in faeces. Only through captive studies can the biases associated with consumption, digestion, and passage of prey be understood, thereby permitting estimates of the composition and size of prey consumed (Prime and Hammond 1987; Dellinger and Trillmich 1988; Harvey 1989).

The extent of otolith digestion depends upon the species of fish consumed and the species of pinniped under consideration (Prime 1979; da Silva and Neilson 1985; Murie and Lavigne 1985; Harvey 1989; Prime and Hammond 1990). For example, Dellinger and Trillmich (1988) recovered 49% of herring otoliths from South American fur seals (*Arctocephalus australis*) but only 34% from California sea lions. Recovery rates of otoliths can also vary widely within a species, as shown by da Silva and Neilson (1985), who recovered only 4% of herring otoliths fed to 1 adult harbour

Table 5. Numbers of fish fed to harbour seals and numbers of structures recovered from seal faeces.

Structure(s)	Herring (1978)	Hake (145)	Pollock (119)	Salmon (1174)	Smelt (1530)	Unknown	Total (4946)
Scale*	6			6	—	> 20000	> 20000
Vertebra†	5574	145	35	6629	799	509	13 691
Eye lens	—	—	—	—		7 963	7 963
Otolith	1179	211	182	1519	707	310	4 108
Prootic – synotic	2572		—	—	—	154	2 726
Atlas -axis*	1398		—	135	—	46	1579
Dentary	10	103	84	52	—		249
Gill raker	—	114	8	81	—	8	211
Tooth		52	—	89		6	147
Ultimate vertebra	138	—	—	—	—		138
Postcleithrum	—	—	133	—			133
Ceratohyal	104	—	—	—			104
Epihyal	83	14	—	—			97
Interopercle	—	—	82	—			82
Pharyngobranchial	—	15	11	20			46
Angular	—	22	15	—	—		37
Quadrate	21	—	—	—			21
Hypobranchial	—	10	10	—			20
Epibranchial	—	—	13	—	—	—	13
Basioccipital	9	—	—	—			9
Hyomandibular	5	—	—	—			5
Total	11099	686	573	8531	1506	> 28 996	> 51379

Note: Structures that were not taxon-specific or digested beyond recognition were classified as unknown. Numbers in parentheses show the number of fish fed.

*Thirty scales were analyzed for taxon and age.

†Excluding the atlas, axis, and ultimate vertebra.

*Identifications of herring include the atlas and axis, otherwise only the atlas.

Table 6. Numbers of structures and elements recovered per fish consumed.

	No. of fish fed	No. of structures/fish	No. of elements/fish
Herring	1978	3.49±0.93	5.61±1.63
Hake	145	4.28±0.65	4.73±2.16
Pollock	119	4.17±0.58	4.82±1.66
Salmon	1174	2.33k0.23	7.27±1.84
Smelt	1530	0.98±0.21	1.08±0.35

Note: Values are given as means ± SD.

seal, compared with 33% recovered from 6 seals by Harvey (1989), and 30% recovered from 4 seals in this study. For gadids, Prime (1979) recovered 86% of the otoliths fed to 1 harbour seal, compared with 73% reported by Harvey (1989) and 74% (pollock and hake) in this study. For salmon, Harvey recovered 62 %, compared with 65% in our study.

Differences in recovery rates probably reflect several factors, including activity levels, enclosure characteristics, access to water (swimming), and feeding methods. A high activity level is associated with increased movement of digesta, so fish do not remain in the stomach and are not exposed to digestive acids as long as in inactive seals (Helm 1979; Dellinger and Trillmich 1988). Our method of allowing harbour seals continuous access to water and a haulout platform was similar to that of Harvey (1989) and yielded rates of otolith recovery that were similar to his.

It is not clear to what extent recovery rates of prey hard parts in captive feeding studies are representative of wild seals, given that the relationships between digestion and seal activity, meal size, frequency of feeding, and prey size are not well understood. In theory, the relative usefulness of different prey hard parts in identifying prey should change little under different digestion rates, even though the total number of taxon-specific elements recovered may change. Thus, our study provides a good measure of the relative usefulness of different taxon-specific hard parts in identifying different prey types in the wild, but may not accurately reflect absolute numbers of structures that might be recovered from scats collected in the wild.

Recovery rates of fish structures during our study are only representative of the prey size class and species used. The size and ontogeny of certain types of fishes are known to affect hard part recovery (da Silva and Neilson 1985; Jobling 1987). For example, adult salmonids and gadids have better developed teeth and branchial structures than do juveniles (R. Wigen, personal communication, 1992). Therefore, structures in adult fish that are diagnostic of taxa may not be morphologically distinct or developed in juvenile fish.

Previous captive-feeding studies have not recorded or

quantified any fish hard parts other than otoliths (Prime 1979; Dellinger and Trillmich 1988; Harvey 1989). Yet otoliths represented only 17 % of all taxon-specific hard parts identified in this study. Vertebrae were the most numerous hard part identified during experimental trials (66% of all taxon-specific hard parts), and were the most important structure for determining the presence or absence of herring, smelt, and salmon. They have long been used to identify fish in archaeological studies (Casteel1976), and are potentially very useful in mammalian diet studies. The abundance of scales in pinniped faeces, and their value for identification and age estimates, also suggests great potential for pinniped diet studies (e.g., Bigg et al. 1990). Our study is the first to examine the diagnostic distinctiveness of scales that have passed through the digestive tract, and the results suggest that additional studies of recovered scales are warranted.

Gill rakers, teeth, and other hard parts were important in confirming prey identifications based on otoliths, vertebrae, and scales. We found that 2-5 structures per fish species represented more than 90% of all elements recovered. This may allow researchers to concentrate identification efforts for certain prey on specific structures. All five experimental prey types averaged at least one structure recovered from each fish consumed. When only the number of otoliths recovered per fish was calculated there was at least a twofold decrease in the number of structures and elements recovered per fish for all prey types. The identification of prey from other hard parts recovered from wild harbour seal scats further emphasizes the importance of using multiple structures. For example, Olesiuk et al. (1990) and Cottrell (1995) found that otoliths were absent in 58 and 55% of prey identifications, respectively.

The time, effort, and money required to set up a reference collection of fish hard parts, combined with the years of training necessary to identify digested fish structures contained in faeces has precluded the widespread use of skeletal structures in prey identification. Fish hard part identification keys are currently limited to a narrow range of species and structures (Fitch and Brownell 1968; Casteel 1976; Harkonen 1986; Cannon 1987; Hansel et al. 1988).

Accurately identifying the size and type of prey consumed by harbour seals is necessary for evaluating intra- and interspecific dietary overlap (Fiscus 1979; Beverton 1985; Lowry and Frost 1985; Gearin et al.[4]; Harwood and Croxall 1988; Bigg et al. 1990). Previous faecal studies estimating the quantitative composition of prey have relied on otolith identification (Prime and Hammond 1987; Pierce et al. 1991). However, using only otoliths or any other single prey hard part provides an incomplete understanding of diet. Seals tearing up large prey during consumption, several seals feeding on the same prey item, and digestive processes all affect prey hard part recovery. Using several prey structures will minimize the likelihood of failing to identify a prey type in faeces and reduce overall subjectivity in prey identifications.

[4] P.J. Gearin, B. Pfeifer, S.J. Jefferies, R.L. DeLong, and M.A. Johnson. Results of the 1986–1987 California sea lion – steelhead trout predation control program at the Hiram M. Chittenden Locks. Unpublished manuscript, National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, Wash.

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