# CLASSIFYING PREY HARD PART STRUCTURES RECOVERED FROM FECAL REMAINS OF CAPTIVE STELLER SEA LIONS (EUMETOPIAS JUBATUS)

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#### ABSTRACT

Feces were collected from six Steller sea lions (Eumetopias jubatus) that consumed known amounts of Atka mackerel (*Pleurogrammus monopterygius*), Pacific herring (Clupea harengus), pink salmon (Oncorhynchus gorbuscha), walleye pollock (Theragra chalcogramma), and squid (Loligo opalacens). The goal was to determine the numbers and types of taxon-specific hard parts that pass through the digestive tract and to develop correction factors for certain abundantly occurring structures. Over 20,000 fish and squid were consumed during 267 d of fecal collection. During this period, over 119,000 taxonspecific hard parts, representing 56 different structures, were recovered. Skeletal structures and non-skeletal structures accounted for 72% and 28% of all hard parts, respectively. The branchiocranium, axial skeleton, and dermocranium regions of the skeletal system accounted for the greatest number of hard parts recovered. Over 70% of all recovered hard parts were represented by one to six taxa specific structures for each prey type. The average number of hard parts (3.1-31.2) and structure types (2.0-17.7) recovered per individual prey varied across taxa and were used to derive correction factors (to reconstruct original prey numbers). A measure of the variability of hard part recovery among sea lions showed no difference for certain herring, pollock, and squid structures, however, there was a significant difference for salmon and Atka mackerel structures. Identifying all taxon-specific prey hard parts increases the likelihood of identifying and estimating the number of prey consumed.

Key words: Steller sea lion, *Eumetopias jubatus*, diet, feces, scat, hard parts, bones, captive feeding, correction factors.

The dramatic decline of Steller sea lions (*Eumetopias jubatus*) in the Gulf of Alaska and Bering Sea has prompted researchers to monitor sea lion diets and explore potential links with changes in prey abundance and availability (Merrick *et al.* 1997, Loughlin 1998). No experiments have been conducted on the recovery rates of hard parts from prey fed to captive Steller sea lions. Passage and recovery rates of hard parts are unknown for this species. This lack of information makes qualitative and quantitative prey consumption estimates from fecal material difficult. Determining the diversity and relative importance of taxon-specific hard parts of the major prey types of Steller sea lions in captive feeding studies will provide researchers with correction factors to improve estimates of the total number and mass of different prey ingested.

Pinniped diet studies are increasingly relying on identifying prey remains found in scats (Olesiuk et al. 1990, Cottrell 1995, Merrick et al. 1997). Scat collection is relatively easy and large sample sizes can be collected from different geographical locations, often at all times of the year. Unlike pinniped stomach analysis where partial or whole prey can be identified, scat analysis relies on identifying partially digested hard parts.

Otoliths, a cranial structure of fish consisting primarily of calcium carbonate, are often found in pinniped stomachs and feces, and have been the primary hard part used to identify the size, type, and number of prey consumed. Mass and size of prey consumed can be estimated from the number and size of otoliths recovered in pinniped feces (Bowen et al. 1993, Tollit et al. 1997). However, there are a number of well-documented limitations of using only otoliths for prey identification (Murie and Lavigne 1985, Jobling and Breiby 1986, Jobling 1987, Murie 1987, Harvey 1989, Pierce and Boyle 1991, Harvey and Antonelis 1994, Cottrell 1995, Cottrell et al. 1996). The presence of a prey type may be missed due to otoliths being damaged, totally digested, digested beyond identification, or not being ingested during prey consumption. A further complication is that some species of fish do not have otoliths suitable for prey identification.

Captive pinniped feeding studies have shown considerable variation in the recovery rates of otoliths in feces (Jobling 1987, Harvey 1989, Cottrell et al. 1996, Tollit et al. 1997, Marcus et al. 1998). These studies show that otolith recovery rates vary among pinniped species for the same prey type, suggesting that recovery rates may be species specific. However, even within a pinniped species, otolith recovery rates can vary due to experimental design (Prime 1979, da Silva and Neilson 1985, Harvey 1989, Cottrell et al. 1996). For example, da Silva and Neilson (1985) used small dry enclosures to hold harbor seals and had otolith recovery rates as low as 4%. Recent otolith recovery studies of captive harbor seals with large saltwater enclosures and haul outs had higher recovery rates. For example, Harvey (1989) recovered 33% herring, 62% salmon, and 73% pollock otoliths, while Cottrell et al. (1996) recovered 30% herring, 65% salmon, and 74% pollock otoliths.

Many factors can affect hard part digestion in pinnipeds, which in turn can alter the numbers and types of hard parts found in pinniped fecal material. Captive studies are unlikely to account for all of the variables that influence

hard part digestion in free-ranging pinnipeds. However, a well-designed study with proper enclosure characteristics (*i.e.*) large saltwater area with haul out) can contribute to our understanding of hard part recovery rates. Identifying taxon-specific and commonly occurring structures will allow researchers to better estimate the numbers and types of prey in pinniped diets.

Only one captive feeding study has so far identified all taxon-specific hard parts recovered from pinniped feces. Cottrell et al. (1996) examined hard parts recovered for five major prey species fed to harbor seals. They found that four to six structures accounted for over 90% of all taxon-specific hard parts. Past studies on captive otariids have estimated recovery rates of otoliths from South American fur seals (Arctocephalus australis) and California sea lions (Zalophus californianus) (Dellinger and Trillmich 1988). However, none have extended this approach to other fish structures or have cross-validated the results from otoliths and other hard parts. Otariids may have lower otolith recovery rates than phocids in controlled captive feeding studies (Dellinger and Trillmich 1988, Harvey 1989). Different size classes of the same prey type can have varying otolith recovery rates (Cottrell et al. 1996, Tollit et al. 1997, Marcus et al. 1998).

The objectives of our study were to (1) identify which taxon-specific hard parts pass through the Steller sea lion digestive tract, (2) determine the numbers of hard parts recovered per fish fed, and (3) calculate correction factors for structures that are useful for estimating the number of fish consumed.

#### **Methods**

# Feeding Experiments

The feeding trials were conducted from November 1994 to August 1996 at the Vancouver Aquarium Marine Science Centre with six 1–3-yr-old Steller sea lions. The sea lions were housed individually in continuously flowing saltwater tanks (5 × 2 × 2 m) equipped with a 1 × 2-m haul-out platform. They consumed 5%–8% of their body mass each day in 5–14-d experiments. Five species of prey were used: Atka mackerel (*Pleurogrammus monopterygius*), Pacific herring (*Clupea harengus*), pink salmon (*Oncorhynchus gorbuscha*), squid (*Loligo opalacens*), and walleye pollock (*Theragra chalcogramma*). Individual sea lions were fed each prey type once for a total of 30 experiments (six sea lions × five species of prey).

Standard lengths and masses of prey were recorded to 5-mm and 0.1-g accuracy, respectively (Table 1). The sea lions were fed fish fillets or headless squid (*i.e.*, no hard parts) 48 h before each trial to allow for the passage of hard parts from previous meals. This was repeated at the end of each trial to ensure that all hard parts consumed during the trial had been passed. All fish or squid hard parts should pass through the digestive tract or be totally digested within 30 h (Helm 1979, Prime 1979, Prime and Hammond 1987, Cottrell *et al.* 1996).

Tanks were drained and cleaned daily by filtering their contents through

Prey	Length (mm)	Mass (g)	n
Atka mackerel	$404.3 \pm 47.3$	$1,131.6 \pm 146$	164
Herring	$178.6 \pm 9.2$	$119.2 \pm 9.7$	7,085
Pollock	$331.4 \pm 30.4$	$484.7 \pm 11.1$	488
Salmon	$472.0 \pm 34.3$	$1,641.9 \pm 165$	370
Squid	$122.6 \pm 10.6$	$47.3 \pm 4.1$	12,669

Table 1. Length and mass (mean  $\pm$  SD) and number of prey fed to Steller sea lions.

0.495-mm nylon mesh fitted to the outflow. Sea lions were restricted to their haul out during tank emptying to prevent the breakage of hard parts. Hard parts from feces were dried and stored in petri dishes until examination. The ability to recover fish structures from the tanks was tested by scattering 20–25 marked vertebrae, otoliths, or postcleithrum from herring, pollock, and salmon into the tank during harbor seal feeding experiments (see Cottrell et al. 1996). All the marked elements were recovered during the next tank cleaning. Thus, we assumed that all fish hard parts passed in feces during the experiments were recovered.

# Identification of Prey Hard Parts

Prey hard parts recovered from scats were compared with a reference collection of identified skeletal and non-skeletal hard parts. Naming of hard parts followed Rojo (1991). Hard parts were identified to the lowest possible taxon and grouped according to anatomical region, number recovered, or percentage recovered. Hard parts digested beyond recognition and/or not diagnostic of taxa were not included in our analysis (e.g., ribs). Structures were separated into two categories (Cottrell et al. 1996):

Category 1: Number and type—structures that could be used to estimate the number of prey consumed, and that represented >10% of the prey consumed (structures that accounted for <10% would be of little use for quantitative estimates).

Category 2: Type only—structures that could be used to identify the species consumed (some hard parts such as scales, teeth, branchials, and gill rakers often have differing numbers per fish or have hundreds of hard parts per fish making estimates of the number of prey ingested intractable) or represented <10% of the total number of prey consumed.

Correction Factors (CF), which must be multiplied by the number of recovered bones to estimate the number of fish consumed, were calculated as

$$CF_{i,x,s} = \frac{N_{x,s}}{I_{i,x,s}}$$

where I is the total number of the structure i that was recovered from the fecal remains of sea lion s. N is the total number of prey species x ingested

by sea lion s. Mean CFs and standard deviations were calculated for each structure and species of prey consumed (n = 6 sea lions).

## RESULTS

## Hard Part Recovery

Over 20,000 fish and squid were consumed during 267 d of fecal collection. During this period, over 119,000 taxon-specific hard parts representing 56 different structures were recovered. The break-down of recovered structures by anatomical region differed among the four species of fish. The most diverse types of hard parts were recovered from the skeletal and non-skeletal integumentary system (Table 2). Skeletal structures accounted for the majority of fish hard parts recovered (72%, all fish species combined), with the branchio-cranium, axial skeleton, and dermocranium regions accounting for the greatest number of hard parts (see Fig. 1 for anatomical region locations). Gill rakers were the most numerous taxon-specific structure recovered, followed by teeth, vertebrae and eye lenses. The three skeletal regions with the most structure types recovered (but not necessarily the greatest number of hard parts) were the branchiocranium, dermocranium, and neurocranium.

Non-skeletal structures represented 28% of all the taxon-specific hard parts recovered (all fish species combined). Although the non-skeletal part of the fish accounted for only three structure types (tooth, eye lens, and otolith), each was present in high numbers (Table 2).

# Prey Identification

Category 1 structures are listed in Table 3 with their corresponding recovery rates. The types of structures useful for predicting prey numbers and their recovery rates varied across taxa. Atka mackerel had only three structures with recovery rates greater than 10%: retroarticular (17%), scapula (14%), and basipterygium (13%). For herring, the top three Category 1 structures were prootic (43%), atlas/axis (21%), and otolith (19%). Pollock had the most Category 1 structures with otolith (72%), postcleithrum (54%), and interopercle (48%) having the highest recovery rates. Salmon had only two Category 1 structures: hypohyal (10%) and otolith (10%). The beak (74%) was the only squid structure useful for quantitative estimates. Correction factors for reconstructing the number of a particular hard part that were ingested were derived for Category 1 structures (Table 4).

The number of eye lenses recovered provided the best estimates for the number of prey ingested for all prey types, 52%–83% of all eye lenses were recovered. Unfortunately, current identification techniques cannot determine prey type from eye lenses.

Category 2 structures and numbers recovered varied across taxa. However, gill rakers, teeth, vertebra, and branchials were useful for almost all prey types and were recovered in the greatest numbers. Teeth were taxon-specific for all prey types except herring.

Table 2. Number of skeletal and non-skeletal hard parts recovered per 100 fish fed. Naming of hard parts follows Rojo (1991).

		Atka mack-	Her_	Pol-	Sal_	
Region	Structure	erel	ring	lock		Total
Non-skeletal						1,816
INOII-SKEICIAI	Tooth	174	0	442	456	1,072
	Eye lens	104	122	167	142	535
	Otolith	7	37	145	20	209
Skeletal						4,769
Neurocranium						296
	Prootic	0	173	12	0	185
	Parasphenoid	0	0	27	0	27
	Exoccipital	4	8	8	0	20
	Basioccipital	0	2	17	0	19
	Sphenotic	0	11	8	0	19
	Prefrontal	0	0	7	0	7
	Supraoccipital	0	3	4	0	7
	Epiotic	0	6	0	0	6
	Opisthotic	0	0	4	0	4
	Pterotic	0	2	0	0	2
Dermocranium						487
	Interopercle	1	1	95	0	97
	Dentary	0	1	77	0	78
	Premaxilla	0	O	70	0	70
	Maxilla	0	1	69	0	70
	Branchial stegal ray	0	0	70	0	70
	Vomer	5	1	14	0	20
	Preopercle	0	2	18	0	20
	Parietal	0	8	9	0	17
	Subopercle	0	1	16	0	17
	Opercle	2	1	10	0	13
	Urohyal	0	2	6	0	8
	Frontal	0	0	7	0	7
Splanchnocranium						304
•	Retroarticular	33	1	74	0	108
	Quadrate	4	3	72	0	79
	Angular	0	1	32	0	33
	Hyomandibular	0	8	23	0	31
	Ectopterygoid	0	0	25	0	25
	Palantine	0	0	17	0	17
	Sympletic	0	0	11	0	11
Branchiocranium						<i>2,</i> 479
	Gill raker	57	6			1,912
	Epi, hypobranchial	59	9	114		182
	Ceratobranch	4		69		78
	Ceratohyal	0				68
	Hypohyal	15	19			68
	Epihyal	0				53
	Pharyngeal plate	7	6			45
	Pharyngobranch	9				42
	Basibranch	11	2			27
	Interhyal	0	0	4	0	4

Table 2. Continued.

Dagian	C	Atka mack-				/r: 1
Region	Structure	erel	ring	lock	mon	Total
Appendicular skeleton						317
	Postcleithrum	0	0	109	0	109
	Posttemporal	0	0	48	O	48
	Supracleithrum	0	0	42	O	42
	Scapula	29	3	4	O	36
	Basipterygium	26	0	6	0	32
	Radial	0	0	0	27	27
	Cleithrum	0	0	19	0	19
	Coracoid	0	0	4	O	4
Axial skeleton						886
	Vertebrae	11	284	205	301	801
	Atlas	0	43	36	0	79
	Penultimate vertebrae	0.	6	0	0	6

Over 70% of hard parts were represented by one to six taxon-specific structures for each prey type (excluding eye lenses). The average number of hard parts (3.1-31.2) and structures (2.0-17.7) recovered per prey item consumed varied among taxa (Table 5).

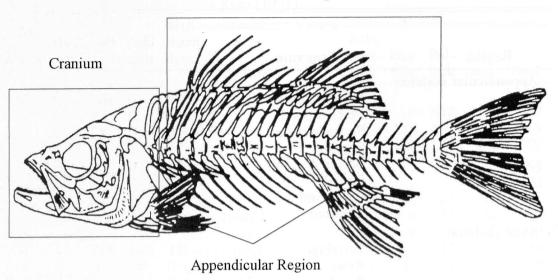
We found no significant differences in the recovery rates of the two most frequently occurring Category 1 structures from herring, pollock, and squid (Table 6). However, the recovery rates of the two most frequently occurring Category 1 structures from Atka mackerel and salmon, differed significantly.

### DISCUSSION

Both skeletal and non-skeletal prey hard parts were useful in identifying prey in Steller sea lion feces. The regions of the fish body that yielded the most taxon-specific hard parts varied with prey type. The appendicular skeleton and non-skeletal regions of Atka mackerel and salmon were the most important areas for hard part recovery. For herring and pollock, the cranial regions and non-skeletal regions had the most taxon-specific structures. These regions have dense bone structures that support musculature and protect vital organs, which make their hard parts particularly resistant to digestion. The dermocranium and splanchnocranium regions of the skeleton contained the majority of Category 1 structures. The variability in bone density and morphology of the same structures across taxa accounted for the varying structure recovery rates among prey species. Even within a prey species, structure recovery rates can vary due to size and ontogenic differences in bone density and morphology between juvenile and adult fish (Cottrell *et al.* 1996).

Category 2 structures, which identify the presence of a prey type (but not the number), were the most numerous hard parts recovered (>80%). For diet estimation methods, such as frequency of occurrence, these are the only struc-

# **Axial Region**



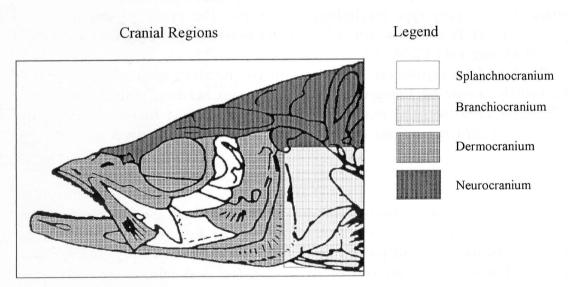


Figure 1. Major skeletal regions from where hard parts were recovered. Branchiocranium region refers to internal branchial area of the fish while external bony portion is dermocranium. Figure adapted from Cannon (1987).

tures researchers need to identify prey in scats. Qualitative measures of pinniped diet are frequently used for prey data from scat analysis (e.g., Pitcher 1980, Green et al. 1990, Olesiuk et al. 1990, Pierce et al. 1991, Cottrell 1995). Quantitative diet methods using prey otoliths have been used to reconstruct the numbers, masses, and lengths of ingested prey for some species of pinnipeds (e.g., Prime and Hammond 1987, Bowen et al. 1993, Tollit and Thompson 1996). Quantitative measures of diet provide researchers and managers with important information regarding the distribution of prey sizes and

numbers that pinnipeds eat which assists with management and conservation decisions. As correction factors are developed for the many types of prey hard parts of different pinniped species, estimates of the total number and mass of prey may be improved.

Category 1 structures must be used if quantitative diet estimation methods are being employed. Category 1 structures provide estimates of the number of different prey types ingested in a fecal unit. Furthermore, correction factors of Category 1 structures derived from captive pinniped feeding studies can be applied to scats collected in the wild to reconstruct absolute numbers and improve estimates of the total mass of prey types ingested. We derived correction factors for three Atka mackerel structures, three herring structures, fifteen pollock structures, two salmon structures, and four beaks recovered from squid. Correction factors should be used with caution, until the many factors that affect the recovery of prey hard parts are better understood and the relationship between captive and wild study results are better known.

We found significant differences in individual sea lion recovery rates of major Category 1 structures for two of the five prey types. This variability in hard part recovery among individuals in controlled experiments indicates that the reconstruction of the total number and mass of prey from feces collected in the wild may be problematic for some prey species. There was no difference in the recovery rates among sea lions for the two highest occurring Category 1 structures for herring, pollock, and squid. The two prey types (Atka mackerel and salmon) that had significantly different structure recovery rates among sea lions had low Category 1 structure recovery rates (10%–17%). This suggests that it would be problematic to reconstruct the absolute number of prey ingested for prey types with low Category 1 structure recovery rates (i.e., <20%). Atka mackerel and salmon also had lower sample sizes which may also explain some of the variability among sea lions.

The varying resistance of prey hard parts to digestion is influenced by the amount of time spent in the stomach. Gastrointestinal mechanisms influencing the movement of pinniped digestia are not well understood. However, studies of dogs found that caloric value was positively related to retention time (Hinder and Kelly 1977). Stomach contents were retained until the initiation of the interdigestive myoelectric complex (IMC) (Code and Marlett 1975). The IMC is a series of powerful stomach contractions that serve to expel material too large to be absorbed from the stomach after digestion ceases. The physiologic processes surrounding the initiation and cessation of the IMC may explain some of the variability in the digestion of prey hard parts. Structure morphology and susceptibility to getting caught in the stomach rugga also affects the digestion of hard parts (Bigg and Fawcett 1985).

The influence of pinniped age, body condition, and parasite load on prey hard part recovery is unknown and requires further study. Pinniped feeding behavior such as frequency of feeding, mass of a feeding, and composition of the meal may also affect hard part recovery (Cottrell *et al.* 1996, Marcus *et al.* 1998). Detailed prey hard part recovery experiments are needed to examine how these variables influence prey hard part digestion.

Table 3. Prey structures that could be used to detect the percentage (Category 1) or presence (P) of a prey (Category 2), [Sample size], (A = absent).

	Atka mackerel	Herring	Pollock	Salmon	Squid
Structure	[164]	[7,085]	[488]	[370]	[12,669]
Non-skeletal					
Tooth	P	Α	P	P	Α
Eye lens	52.0	60.9	83.3	70.8	81.4
Otolith	P	18.6	72.3	10.0	Α
Squid beak	Α	Α	Α	Α	73.8
Skeletal					
Neurocranium					
Prootic	Α	43.3	P	Α	Α
Parasphenoid	Α	A	P	Α	Α
Exoccipital	A	P	P	Α	Α
Basioccipital	Α	P	P	Α	Α
Sphenotic	Α	P	P	Α	Α
Prefrontal	Α	Α	P	Α	Α
Supraoccipital	Ā	P	P	A	Α
Epiotic	Α	P	Α	Α	Α
Opisthotic	Α	. A	P	Α	Α
Pterotic	Α	P	Α	Α	Α
Dermocranium					
Interopercle	P	P	47.6	Α	Α
Dentary	Â	$ { ilde{ ext{P}}}$	38.4	Ā	Ā
Premaxilla	Â	Ā	35.2	Ā	A
Maxilla	A	P	34.3	Ã	Ā
Branchial stegal ray	Ā	Â	P	Ā	Ā
Vomer	Ã	P	P	Ā	Α
Preopercle	Ā	P	P	A	Α
Parietal	Ā	P	P	Α	Α
Subopercle	A	P	P	Α	Α
Opercle	P	P	P	Α	Α
Urohyal	Ā	P	P	Α	Α
Frontal	A	P	P	Α	Α
Splanchnocranium					
Retroarticular	16.5	P	37.2	A	Α
Quadrate	P	P	35.9	A	Ā
Angular	Ã	P	16.1	Ā	A
Hyomandibular	Ā	P	11.7	A	Α
Ectopterygoid	Ā	Ā	P	Α	Α
Palantine	Ā	A	P	Α	Α
Sympletic	A	Α	P	Α	$\mathbf{A}^{-1}$
Branchiocranium					
Gill raker	P	P	P	P	Α
Epi, hypobranchial	P	P	P	Â	Ä
Ceratobranch	P	P	P	A	A .
Ceratobranen	Å	P	33.1	A	A
Hypohyal	A	P	P	10.3	Ä
Epihyal	A	P	22.8	A	Â
Pharyngeal plate	P	P	P P	A	A
Pharyngobranch	P	P	P	A	Ā
	~				
Basibranch	P	P	P	Α	Α

Table 3. Continued.

Structure	Atka mackerel [164]	Herring [7,085]	Pollock [488]	Salmon [370]	Squid [12,669]
Appendicular skeleton					
Postcleithrum	Α	Α	54.4	Α	Α
Posttemporal	Α	P	23.9	Α	Α
Supracleithrum	Α	P	21.1	Α	Α
Scapula	14.4	P	$\mathbf{P}$	Α	: A
Basipterygium	13.0	Α	P	Α	Α
Radial	Α	Α	Α	P	Α
Cleithrum	Α	Α	P	Α	Α
Coracoid	Α	Α	P	Α	Α
Axial skeleton					
Atlas	Α	21.4	36.3	Α	Α
Other vert.	P	P	P	P	Ā
Penultimate vert.	Ā	P	Ā	Ā	Ā

Table 4. Correction factors for prey hard parts recovered in feces from six captive Steller sea lions. The correction factor (CF) when multiplied by number of a hard part recovered in feces provides estimate of total number of that prey species ingested. Values given as means  $\pm$  SD.

Species	Structures	CF
Atka mackerel	Retroarticular Scapula Basipterygium	$3.09 \pm 1.42$ $3.47 \pm 1.55$ $3.88 \pm 1.62$
Herring	Prootic/Synootic Atlas/axis Otolith	$0.59 \pm 0.06$ $2.34 \pm 0.08$ $2.43 \pm 0.56$
Pollock	Otolith Postcleithrum Interopercle Dentary Retroarticular Premaxilla Quadrate Maxilla Ceratohyal Posttemporal Epihyal Atlas Supracleithrum Angular Hyomandibular	$0.70 \pm 0.08$ $1.03 \pm 0.24$ $1.22 \pm 0.34$ $1.46 \pm 0.47$ $1.49 \pm 0.67$ $1.58 \pm 0.55$ $1.72 \pm 0.66$ $1.79 \pm 0.78$ $1.92 \pm 0.98$ $2.41 \pm 0.77$ $2.44 \pm 0.67$ $3.25 \pm 1.25$ $3.67 \pm 2.45$ $4.77 \pm 1.33$ $4.97 \pm 1.47$
Salmon	Hypohyal Otolith	$4.96 \pm 1.87$ $4.99 \pm 2.12$
Squid	Beak	$0.70 \pm 0.11$

Table 5.	Average	number	of	hard	parts	and	hard	part	types	recovered	per	fish
consumed (±	= SD).											

	Average number recovered per prey				
Prey	Hard parts	Hard part structures			
Atka mackerel	$4.5 \pm 0.8$	$3.8 \pm 0.5$			
Herring	$7.9 \pm 1.9$	$5.0 \pm 0.5$			
Pollock	$31.2 \pm 6.1$	$17.7 \pm 2.7$			
Salmon	$19.5 \pm 3.6$	$4.7 \pm 1.5$			
Squid	$3.1 \pm 0.2$	$2.0 \pm 0.1$			

We found that one to six structures for each prey type represented more than 70% of all hard parts recovered (excluding eye lenses). This may allow researchers to concentrate identification efforts for certain prey to specific structures. Each prey type had at least three structure types and five hard parts recovered per fish ingested. Although herring had fewer hard parts recovered per fish than pollock or salmon when the number of fish ingested in a typical meal was calculated, the number of hard parts recovered per species per meal was greater for herring. Larger prey items may be missed or underrepresented if all prey hard parts are not identified.

The only other study to recover and identify all hard parts from captive pinnipeds was conducted by Cottrell et al. (1996). They identified taxon-specific hard parts recovered from five major prey types of harbor seals. Three prey types were common to our study: herring, pollock, and salmon. The herring were similar sizes and weights in both studies. The order of the four most abundant herring structures recovered (vertebrae, prootic, atlas, otolith) were the same. However, Category 1 structure recovery rates were lower for Steller sea lions than for harbor seals: atlas (21% vs. 35%), prootic (21% vs. 33%) and otolith (19% vs. 30%). Otariid digestive tracts are longer than phocids (Helm 1979) which may negatively affect prey hard part recovery.

*Table 6.* Recovery rates of the two most frequently occurring Category 1 fish structures from different sea lions (n = 6).

Species	Structures	df	$\chi^2$	P
Atka mackerel	Retroarticular Scapula	5	25.72	< 0.001
Herring	Prootic Atlas	5	5.03	0.43
Pollock	Otolith Postcleithrum	5	10.71	0.06
Salmon	Otolith Hypohyal	5	29.80	< 0.001
Squid	Eye lens Beak	5	4.58	0.47

For pollock, the four most frequently recovered Category 1 structures were the same for both pinniped species (otolith, post cleithrum, interopercle, dentary). Recovery rates were slightly lower for Steller sea lions for all structures except interopercle. The number of Category 1 structures (*i.e.*, those that represent >10% of the prey ingested) was much higher for Steller sea lions (16 structures) vs. harbor seals (four structures). This is probably due to the much larger pollock ( $\bar{x}=465$  g) fed to the Steller sea lions than the harbor seals ( $\bar{x}=293$  g).

Salmon otolith recovery rates were very different (10% for Steller sea lions vs. 62% for harbor seals). Smolt sized salmon ( $\bar{x} = 143$  g) were fed to harbor seals while large ( $\bar{x} = 450$  g) salmon were fed to Steller sea lions making direct comparisons difficult. The Steller sea lions ingested the larger salmon whole, but may have damaged the otoliths and decreased recovery rates by biting the head to soften the salmon before ingesting it.

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, Rojo 1991). This, combined with the years of training necessary to identify digested fish structures contained in feces, has precluded the widespread use of all taxon-specific hard parts in prey identification. Focusing identification efforts to specific abundant taxon-specific fish structures may reduce the labor required to identify all prey types present in fecal samples and through the use of correction factors, improve the estimates of the total number of prey ingested.

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## LITERATURE CITED

Bigg, M. A., and I. Fawcett. 1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). Pages 285–291 in J. R. Beddington, R. J. H. Beverton and D. M. Lavigne, eds. Marine mammals and fisheries. George Allen and Unwin Publishing, London, U.K.

Bowen, W. D., J. W. Lawson and B. Beck. 1993. Seasonal and geographic variation in the diet of grey seals (*Halichoerus grypus*) on the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 50:1768–1778.

- Cannon, D. Y. 1987. Marine fish osteology. A manual for archaeologists. Department of Anthropology, Simon Fraser University. Publication No. 18. 133 pp.
- Castell, R. W. 1976. Fish remains in archaeology and paleo-environmental studies. Academic Press, London.
- Code, C. F., and J. A. Marlett. 1975. The interdigestive myoelectric complex of the stomach and small bowel of dogs. American Journal of Physiology 246:289–309.
- Cottrell, P. E. 1995. Diet, activity budgets and movement patterns of harbor seals (*Phoca vitulina*) in Cowichan Bay and adjacent areas. M.Sc. thesis, University of Victoria, Victoria, BC. 118 pp.
- COTTRELL, P. E., A. W. TRITES AND E. H. MILLER. 1996. Assessing the use of hard parts in faeces to identify harbor seal prey: Results of captive-feeding trials. Canadian Journal of Zoology 74:875–880.
- DA SILVA, J., AND J. D. NEILSON. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Canadian Journal of Fisheries and Aquatic Science 42:1439–1442.
- Dellinger, T., and F. Trillmich. 1988. Estimating diet composition from scat analysis of otariid seals (Otariidae): Is it reliable? Canadian Journal of Fisheries and Aquatic Science 42:1865–1870.
- FITCH, J. E., AND R. L. Brownell. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. Fisheries Research Board of Canada 25: 2561–2574.
- Green, K., R. Williams, K. A. Handasyde, H. R. Burton and P. D. Shaughnessy. 1990. Interspecific and intraspecific differences in the diet of fur seals, *Arctoce-phalus* species (Pinnipedia: Otariidae) at Macquarie Island. Australian Mammals 13:193–200.
- Hansel, H. C., S. D. Duke, P. T. Lofty and J. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transcontinental. American Fisheries Society 117:55–62.
- HARKONEN, T. J. 1986. Guide to the otoliths of the bony fishes of the northeast Atlantic. Danbiu ApS., Biological Consultants, Hellrup, Denmark.
- HARVEY, J. T. 1989. Assessment of errors associated with harbor seal (*Phoca vitulina*) faecal sampling. Journal of Zoology, London 219:101–111.
- HARVEY, J. T., AND G. A. ANTONELIS. 1994. Biases associated with non-lethal methods of determining the diet of northern elephant seals. Marine Mammal Science 10: 178–187
- Helm, R. C. 1979. Initial defecation time and intestinal length of three species of pinnipeds: *Phoca vitulina, Zalophus californianus*, and *Mirounga angustirostris*. M.A. thesis, California State University, CA. 89 pp.
- HINDER, R. A., AND K. A. KELLY. 1977. Canine gastric emptying of solids and liquids. American Journal of Physiology 233:235–240.
- JOBLING, M. 1987. Marine mammal faeces samples as indicators of prey importance: A source of error in bioenergetics studies. Sarsia 72:255–260.
- JOBLING, M., AND A. Breiby. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia 71:265–274.
- LOUGHLIN, T. R. 1998. The Steller sea lion: A declining species. Biosphere Conservation 1:91–98.
- Marcus, J., W. D. Bowen and J. D. Eddington. 1998. Effects of meal size on otolith recovery from fecal samples of gray and harbor seal pups. Marine Mammal Science 14:789–802.
- MERRICK, R. L., M. K. CHUMBLY AND G. V. BYRD. 1997. Diet diversity of Steller sea lion (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. Canadian Journal of Fisheries and Aquatic Science 54:1342–1348.
- MURIE, D. J. 1987. Experimental approaches to stomach content analysis of piscivorous marine mammals. Pages 147–163 in A. C. Huntly, D. P. Costa, G. A. J. Worthy

- and M. A. Castellini, eds. Approaches to marine mammal energetics. Special Publication No. 1, The Society for Marine Mammalogy, Lawrence, KS.
- MURIE, D. J., AND D. M. LAVIGNE. 1985. Digestion and retention of Atlantic herring otoliths in the stomachs of grey seals. Pages 292–299 in J. R. Beddington, R. J. H. Beverton and D. M. Lavigne, eds. Marine mammals and fisheries. George Allen and Unwin, Publishing, London.
- OLESIUK, P. F., M. A. BIGG, G. M. ELLIS, S. J. CROCKFORD AND R. J. WIGEN. 1990. An assessment of the feeding habits of harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Canadian Technical Report, Fisheries and Aquatic Science No. 1730. 13 5pp.
- PIERCE, G. J., AND P. R. BOYLE. 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanographic Marine Biology 29:409–486.
- PIERCE, G. J., P. M. THOMPSON, A. MILLER, S. W. DIACK, D. MILLER AND P. R. BOYLE. 1991. Seasonal variation in the diet of common seals (*Phoca vitulina*) in the Mory Firth area of Scotland. Journal of Zoology, London 223:641–652.
- PITCHER, K. W. 1980. Food of the harbor seal, *Phoca vitulina*, in the Gulf of Alaska. Fisheries Bulletin, U.S. 78:544–549.
- PRIME, J. H. 1979. Observations on the digestion of some gadid fish otoliths by a young common seal. International Council for the Exploration of the Sea. C.M. 1979/N14.
- PRIME, J. H., AND P. S. HAMMOND. 1987. Quantitative assessment of grey seal diet from faecal analysis. Pages 165–185 in A. C. Huntly, D. P. Costa, G. A. J. Worthy and M. A. Castellini, eds. Approaches to marine mammal energetics. Special Publication No. 1, The Society for Marine Mammalogy, Lawrence, KS.
- ROJO, A. L. 1991. Dictionary of evolutionary fish osteology. CRC Press, Boca Raton, FL. Tollit, D. J., and P. M. Thompson. 1996. Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. Canadian Journal of Zoology 74:1110–1121.
- Tollit, D. J., M. J. Steward, P. M. Thompson, G. J. Pierce, M. B. Santos and S. Huges. 1997. Species and size difference in the digestion of otoliths and beaks: Implications for estimates of pinniped diet composition. Canadian Journal of Fisheries and Aquatic Science 54:105–119.

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