A method to improve size estimates of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by pinnipeds: digestion correction factors applied to bones and otoliths recovered in scats

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Abstract—The lengths of otoliths and other skeletal structures recovered from the scats of pinnipeds, such as Steller sea lions (*Eumetopias jubatus*), correlate with body size and can be used to estimate the length of prey consumed. Unfortunately, otoliths are often found in too few scats or are too digested to usefully estimate prey size. Alternative diagnostic bones are frequently recovered, but few bone-size to prey-size correlations exist and bones are also reduced in size by various degrees owing to digestion. To prevent underestimates in prey sizes consumed techniques are required to account for the degree of digestion of alternative bones prior to estimating prey size. We developed a method (using defined criteria and photo-reference material) to assign the degree of digestion for key cranial structures of two prey species: walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*). The method grades each structure into one of three condition categories; good, fair or poor. We also conducted feeding trials with captive Steller sea lions, feeding both fish species to determine the extent of erosion of each structure and to derive condition-specific digestion correction factors to reconstruct the original sizes of the structures consumed. In general, larger structures were relatively more digested than smaller ones. Mean size reduction varied between different types of structures (3.3–26.3%), but was not influenced by the size of the prey consumed. Results from the observations and experiments were combined to be able to reconstruct the size of prey consumed by sea lions and other pinnipeds. The proposed method has four steps: 1) measure the recovered structures and grade the extent of digestion by using defined criteria and photo-reference collection; 2) exclude structures graded in poor condition; 3) multiply measurements of structures in good and fair condition by their appropriate digestion correction factors to derive their original size; and 4) calculate the size of prey from allometric regressions relating corrected structure measurements to body lengths. This technique can be readily applied to piscivore dietary studies that use hard remains of fish.

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Prey skeletal remnants from stomach samples and more recently from fecal (scat) samples are widely used to determine what pinnipeds eat (Pitcher, 1981; Olesiuk et al., 1990; Tollit and Thompson, 1996; Browne et al., 2002). Prey can usually be identified from taxon-specific hard remains, the sizes of which often correlate with the length and mass of the prey (Härkönen, 1986; Desse and Desse-Berset, 1996). In the past, sagittal otoliths were commonly used to estimate prey size (Frost and Lowry, 1981) but were recognized to erode or become completely digested (Prime and Hammond, 1987; Harvey, 1989). Thus, otolith measurements likely underestimated sizes and numbers of fish ingested (Jobling and Breiby, 1986), thereby preventing a reliable assessment of overlap of prey consumed with catch taken by commercial fisheries (Beverton, 1985). Accurate estimates of size of prey consumed by pinnipeds are also important in order to understand foraging behavior and to explain spatial and temporal variability in diet composition.

There are at least three potential ways to deal with the effect of digestion on estimates of prey size. One is to measure only relatively uneroded otoliths and assume that eroded otoliths are from the same size fish as uneroded otoliths (Frost and Lowry, 1986; Bowen and Harrison, 1994). Another is to apply a single species-specific digestion coefficient or correction factor (DCF), derived from feeding experiments with captive seals fed fish of known sizes and using measurements of all the eroded otoliths recovered in the scats produced (Prime and Hammond, 1987; Harvey, 1989). The third is to estimate and correct for the degree of digestion (based on defined losses of morphological features) of each recovered otolith by using estimates from reference material (Sinclair et al., 1994; Antonelis et al., 1997) or by applying condition-specific DCFs derived from fish fed in captive seal feeding studies (Tollit et al., 1997).

Of the three approaches to correctly estimate prey size from skeletal remains, there is the assumption with the use of only uneroded otoliths that recovery and the degree of digestion is independent of otolith size, resulting in a potentially biased fraction. For certain species it can also result in a notable reduction in sample size because relatively few otoliths pass through the gut in good condition. The second approach of applying mean species-specific DCFs is an improvement to not accounting for size reduction (Laake et al., 2002); however, there is the assumption with this approach that all structures are reduced in size by the same amount. Consequently, mean fish mass may be overestimated if such correction factors are applied to relatively undigested otoliths, or they may be underestimated if applied to very digested otoliths (Hammond et al., 1994; Tollit et al., 1997). The third method accounts for the intraspecific variation in size reduction caused by digestion, reduces systematic error (see Hammond and Rothery, 1996), yields estimates of mass that compare favorably to those fed to captive animals (Tollit et al., 1997), and hence may well be the most promising approach to reconstructing prey size.

The dramatic decline of the western population of Steller sea lions (*Eumetopias jubatus)* in the 1980s (Loughlin et al., 1992; Trites and Larkin, 1996) has prompted a number of studies to determine what they eat and the extent of dietary overlap (prey consumed) with catch taken by commercial fisheries. Stomach contents analysis was used to determine diet until the late 1980s when scat analysis became the preferred method (e.g., Pitcher, 1981; Frost and Lowry, 1986; Sinclair and Zeppelin, 2002). However, unlike in stomachs, there is an overall sparsity of otoliths in Steller sea lion scats (Sinclair and Zeppelin, 2002) and, therefore there is a need to also use other skeletal structures to describe the size of prey consumed.

The following outlines a method (using defined criteria and photo-reference material) to assign the degree of digestion for otoliths and alternative key skeletal structures of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius)* recovered from scats. We also present the results of a feeding study with captive Steller sea lions used to determine the extent of erosion and to derive condition-specific digestion correction factors to reconstruct the original sizes of the pollock and Atka mackerel structures consumed. Finally, we combine these DCFs with newly developed regression formulae that estimate fish length to derive a more accurate method of estimating size of pollock and Atka mackerel consumed by Steller sea lions and other pinnipeds (see Zeppelin et al., 2004, this issue; Tollit et al., 2004, this issue).

Materials and methods

Experimentally derived digestion correction factors

Feeding experiments were conducted with two 3-year-old female Steller sea lions: Steller sea lion 1 [SSL1] [ID no. F97HA], mean mass 129 kg; steller sea lion 2 [SSL2] [ID no. F97SI], mean mass 150 kg) between October 2000 and April 2002 at the Vancouver Aquarium Marine Science Centre. Over the experimental period, the sea lions were fed pollock for 52 days in 16 separate feeding experiments, and Atka mackerel for 31 days in 5 separate feeding experiments, at between ~4–8% of body mass per day. Fork length (FL) and weight of all fish were measured to ±0.1 cm and ±1 g. Sea lions were fed meals of pollock of three size categories (small, 28.5–32.5 cm FL; medium, 33.5–38.7 cm FL; large, 40–45 cm FL) and meals of Atka mackerel of one size category (30–36 cm FL). Fish of one particular size category were fed either as a single meal or as a seven-day block of meals. Full details of a typical experimental protocol can be found in Tollit et al. (2003). Size ranges for any category of fish fed within separate experiments were usually ≤3 cm. Fecal material was collected until no other remains of experimental meals were found (7 days after feeding), and was washed through a 0.5-mm sieve to remove hard parts. Each animal was maintained on whole Pacific herring (*Clupea pallasi*) between experiments at ~6% body mass per day.

The strong relationship between fish size and otolith size also exists for other skeletal structures (Desse and Desse-Berset, 1996). Thus, we quantified the types and numbers of the prey structures recovered in the scats of free-ranging Steller sea lions (from the collections of Trites et al.[1] and Sinclair and Zeppelin, 2000) and selected seven of the most commonly occurring structures for pollock and Atka mackerel. These were the sagittal otolith (OTO), as well as the interhyal (INTE), hypobranchial 3 (HYPO), pharyngobranchial 2 (PHAR), angular (ANGU), quadrate (QUAD), and the dentary (DENT). The structures selected also had particular morphological features that seemed to be relatively resistant to digestion and could effectively be used to estimate fish size (Figs. 1 and 2, Table 1).

Concurrent with our feeding study, we measured selected structures (Figs. 1 and 2) from randomly subsampled fresh fish and combined these data with unpublished NMFS data to generate allometric regression formulae relating structural measurements to fish length (see Zeppelin et al., this issue). Fork lengths (±0.1 cm) and weights (±1 g) of an extended subsample of pollock (8.3–47.7 cm FL) were measured to generate an appropriate regression formula for estimating fish mass from fork length estimates. All selected structures are located in the cranium as illustrated in Zeppelin et al. (2004, this issue). Naming of fish structures follows Rojo (1991).

Initial inspection of selected structures found in scats from the wild revealed high intraspecific variation in the degree of digestion, ranging from no apparent size reduction to about a 60% size reduction (heavily digested material). Consequently, we extended the condition-

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[1] Trites, A. W., D. G. Calkins, and A. J. Winship. 2003. Unpubl. data. Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, Hut B-3, 6248 Biological Sciences Road, Vancouver, B.C., Canada, V6T 1Z4.

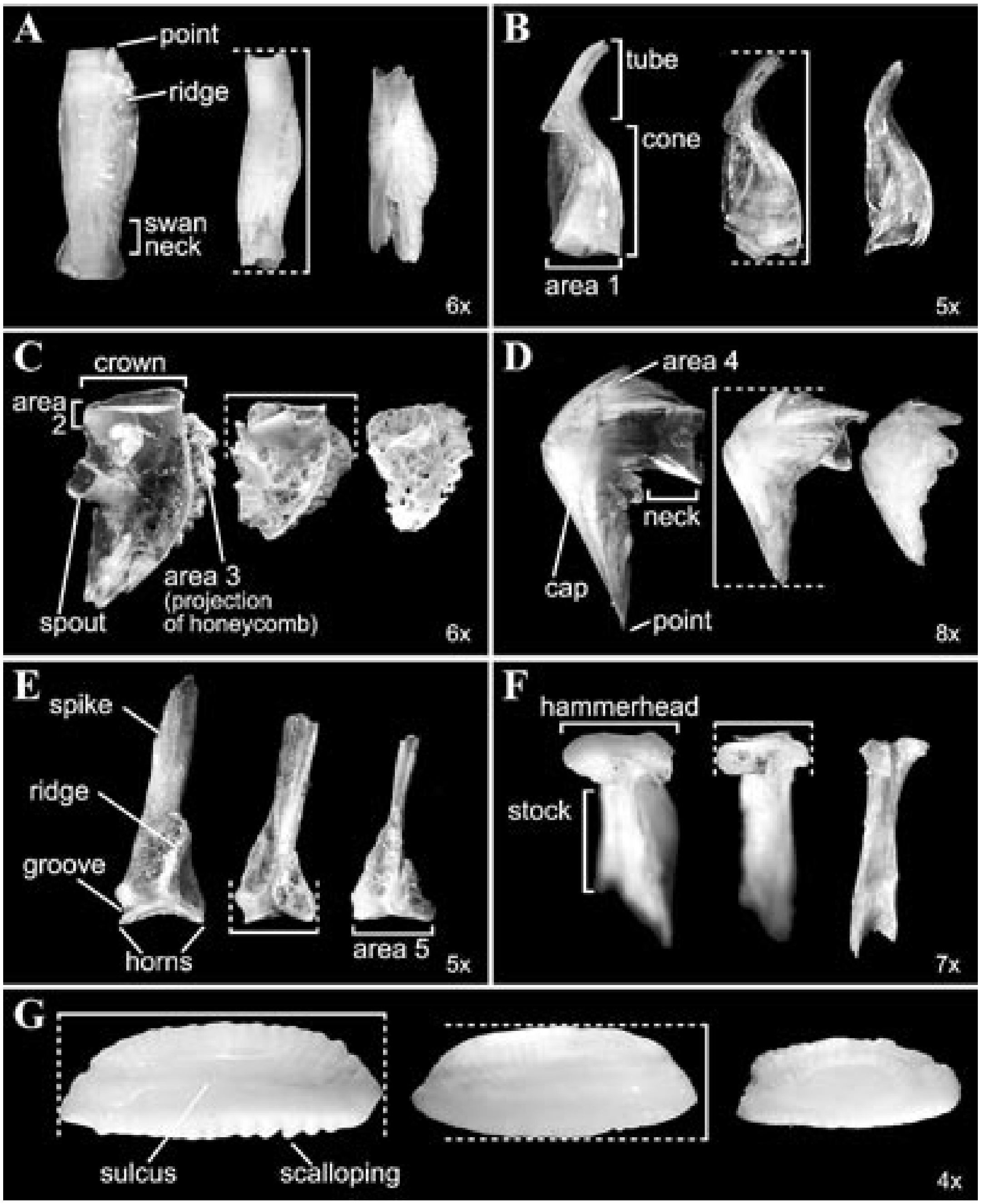

Figure 1

Photographs showing the changes in morphological features in seven cranial structures of walleye pollock (*Theragra chalcogramma*) resulting from digestion. Within each section of the figure three condition categories (good, fair, and poor) are represented from left to right for (**A**) interhyal (INTE), (**B**) hypobranchial 3 (HYPO), (**C**) pharyngobranchial 2 (PHAR), (**D**) angular (ANGU), (**E**) quadrate (QUAD), (**F**) dentary (DENT) and (**G**) sagittal otolith (OTO). Key features used in classification are labeled (see Table 1 for details), and the measurements taken to calculate fish length (solid line between dashed lines).

specific DCF technique described by Tollit et al. (1997). We began by examining the external morphological features and surface topography of selected structures from undigested fish (<12 cm to >53 cm) and compared these with the topography of the same structures recovered from scats collected from wild and captive animals

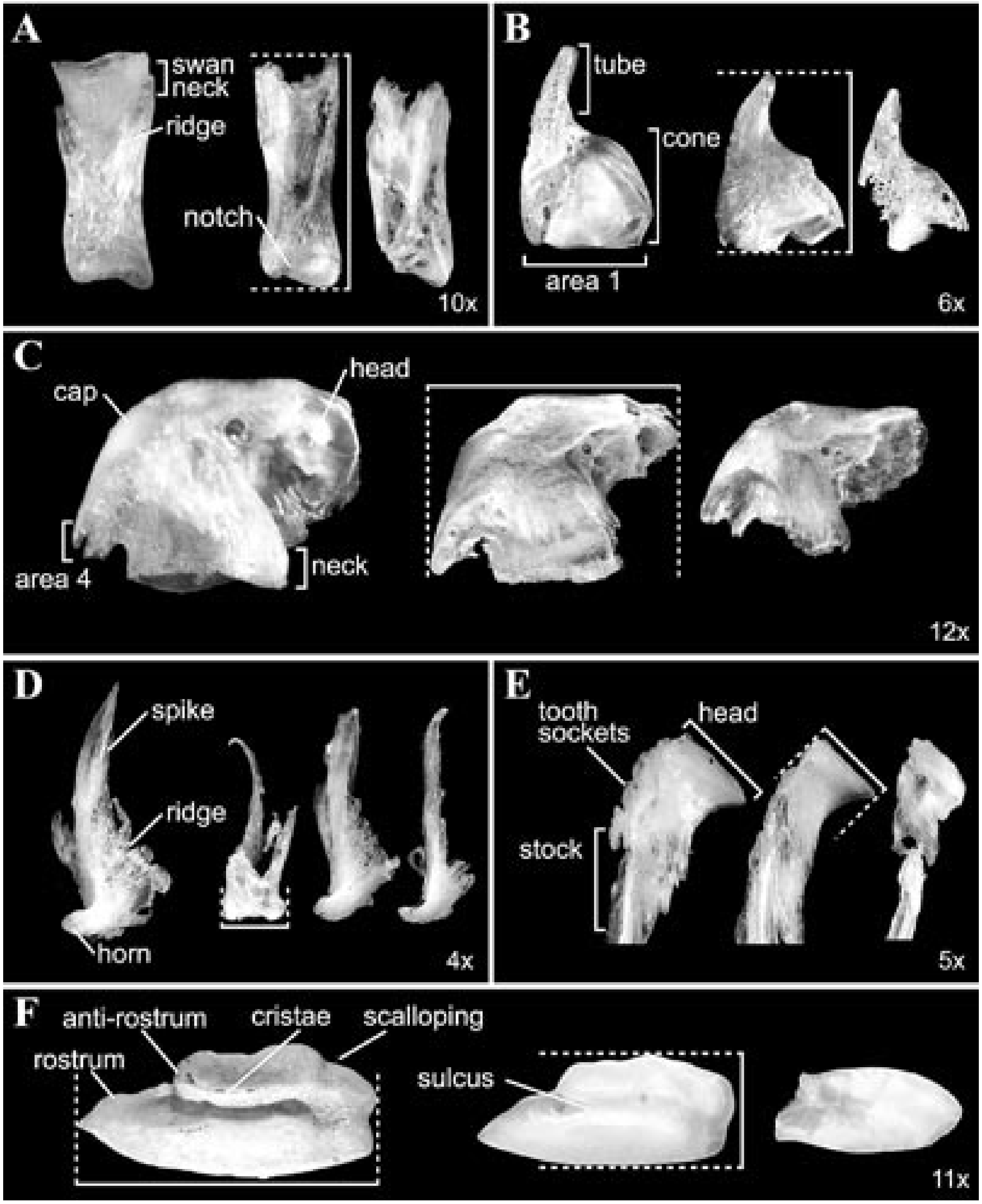

Figure 2

Photographs showing the changes in morphological features in seven cranial structures of Atka mackerel (*Pleurogrammus monopterygius*) resulting from digestion. Within each section of the figure three condition categories (good, fair, and poor) are represented from left to right for (**A**) interhyal (INTE), (**B**) hypobranchial 3 (HYPO), (**C**) angular (ANGU), (**D**) quadrate (QUAD), (**E**) dentary (DENT) and (**F**) sagittal otolith (OTO). Key features used in classification are labeled (see Table 1 for details) and measurements taken to calculate fish length (solid line between dashed lines).

(Figs. 1 and 2). The morphological features used to assess level of digestion showed no differences in relative shape, structure, or in proportion across the size range of fresh fish examined. We then devised a criteria-based method to assign a condition category to each structure depending on the degree of digestion. These criteria take into account only the loss of size to the relevant feature being measured to estimate fish length (Figs. 1 and 2).

The grading criteria for otoliths (OTO) were based on the condition categories developed by Sinclair et al. (1996) to investigate prey selection by northern fur seals (*Callorhinus ursinus*). As seen in Sinclair et al. (1996) and other studies (Frost and Lowry, 1986; Tollit et al., 1997), external features such as lobation and the general shape and definition of the sulcus were found in our study to be good indicators of the degree of otolith digestion. For the remaining cranial bones, digestion indicators included the loss of definition or breakage of defined structural features such as the horns and ridge (QUAD), hammerhead and stock (DENT), swan neck, notch and ridge (INTE), honeycomb and crown (PHAR), cap, neck, and head (ANGU) and tube and cone (HYPO). We used changes in the described condition-category criteria (see Table 1 for full details) in tandem with photo-reference material (Figs. 1 and 2) to classify all structures into one of three digestion grades or condition categories: "good", "fair," or "poor."

Hard parts recovered from feeding experiments were sorted, and all selected cranial structures were assigned a condition category and measured with calipers to within ±0.01 mm. Because otoliths were often chipped or partly broken lengthwise, both length and width were measured. To test our grading technique, an independent observer (T.Z.) reassigned a random subsample of each condition category of pollock structures (n=158) in a blind test.

On initial investigation, high intraspecific variation was observed within the selected structures assigned in poor condition in our feeding study with captive Steller sea lions. Consequently, structures in poor condition were not used to calculate DCFs for this category. Our basis for exclusion was supported by the work of Sinclair et al. (1994) and Tollit et al. (1997). Captive sea lions in our study occasionally regurgitated prey in the swim tank. Recovered structures that we considered to have been regurgitated were excluded from DCF calculations (i.e., vertebrae still articulated, bones that had flesh attached or that were of a size to exclude passage through the pyloric sphincter).

Mean reduction (MR) in the metric of each structure (s) recovered from our feeding experiment was estimated for each remaining condition category (c) according to

$$MR_{s,c} = \left(1 - \frac{\bar{E}_{s,c}}{\bar{I}_s}\right) \times 100,$$

where the mean size of egested structures ($\bar{E}$) of each condition category was calculated from measurements of those recovered from the captive feeding experiments, and the mean size of each ingested structure ($\bar{I}_s$) was estimated from the fork length of fish fed by using inverse predictions of the regression formulae derived from fresh material (Zeppelin et al., 2004, this issue). Mean ingested size was estimated by using bootstrap simulations (1000 runs) that randomly sampled with replacement and selected the median (500$^{\text{th}}$ value) from the sorted bootstrapped values (Reynolds and Aebischer, 1991).

For pollock, mean reduction for each condition category was compared across size ranges by using a Kruskal-Wallis analysis of variance. A significance level of $P<0.0056$ was set based on the Bonferroni adjusted probability for nine multiple comparisons (Siegel and Castellan, 1988). Failing to find any significant differences resulted in pooling the data from each size range to calculate specific condition category MR values. Condition category DCFs were calculated for each selected structure as $\bar{I}_s/\bar{E}_{s,c}$ except for PHAR structures of Atka mackerel because too few elements were recovered from the scats of captive animals.

Estimating confidence limits around digestion correction factors

We used a bootstrap simulation to estimate upper and lower bounds of the 95% confidence interval (CI) given that the DCF is a ratio of two means (Reynolds and Aebischer, 1991). This technique allows different sources of error to be combined or partitioned. There were two major sources of error associated with calculating DCFs (Tollit et al., 1997). The first were those associated with the regression formulae used to calculate the mean size of structure ingested from the original fish fed, and the second were those associated with the errors around the mean size of egested structure (i.e., resampling errors).

We assessed errors associated with the regression formulae using a parametric bootstrapping procedure (Manly, 1997) that involved regressing structure size against fork length. This was repeated 1000 times and 95% confidence intervals were taken as the 25$^{\text{th}}$ and 975$^{\text{th}}$ values of the sorted bootstrapped regression coefficient values. Results were compared to those computed analytically by using the resultant standard error (Eq. 17.23 in Zar, 1984) and were found to be consistent (see Zeppelin et al., 2004, this issue).

We estimated resampling errors related to the variability in digestion of egested structures by repeatedly selecting n structures, at random, with replacement from the original sample set of n egested structures. Mean egested size was recalculated in this way 1000 times, as were a mean DCF and 95% CI as described above. Both regression and resampling errors were combined in sequence to derive overall 95% CIs around DCFs.

Our recommended procedure for applying our DCFs to cranial structures recovered from scats collected in the wild has four steps: 1) measure the recovered structures and grade the extent of digestion using defined criteria and photo-reference collection; 2) exclude structures graded in poor condition; 3) multiply measurements of structures in good and fair condition by their appropriate digestion correction factors to derive their original size; and 4) calculate the size of prey from allometric regressions relating corrected structure measurements to fish fork lengths (see also Tollit et al., 2004, this issue).

Results

A relatively objective method to estimate the degree of digestion of dominant structures of pollock and Atka mackerel was derived by using defined criteria (Table 1) and photo-reference material (Figs. 1 and 2). Condition-specific digestion correction factors (and derived confidence intervals) calculated for each structure augmented our method of estimating size of prey from bones and otoliths recovered in scats, as well as potentially from bones and otoliths taken from stomach contents.

Mean reduction (MR) in the size of pollock DENT and QUAD in good condition and ANGU, HYPO, INTE, OTO, and PHAR in fair condition were between 12.2–18.5%, and larger values were found for QUAD (22.8%) and DENT (24.7%) in fair condition (Table 2). Our overall 95% confidence intervals were generally symmetrical and converted to a mean range of ±2.2% (±0.5, SD) around MR values. Mean DCFs ranged between 1.14 and 1.33, and lower bounds of 95% CIs exceeded 1.11 in all instances, confirming that egested structures of these condition categories were significantly smaller than the size at which they were ingested (Table 2). Partitioning errors showed that resampling of egested structures was the major source of error (>73% across structures) within the overall total. Our overall 95% CIs resulted in a maximum total error of ±1.7 cm around an estimated mean of 40 cm for pollock.

Mean reduction in the size of Atka mackerel structures varied more widely (3.3–26.3%), leading to DCFs ranging between 1.03 and 1.36. QUAD in good condition provided the smallest DCF, and DENT in fair condition the largest. Overall, our 95% CIs converted to a mean range of ±2.4% (±0.6) around MR values, and all lower 95% CI bounds exceeded 1.0 (Table 2). As seen when errors were partitioned for pollock, errors owing to resampling of egested structures were the major source of error (>83% across structures) within the overall total for Atka mackerel. Our overall 95% CIs resulted in a maximum total error of ±1.2 cm around an estimated mean of 40 cm for Atka mackerel.

With the exception of the two largest skeletal structures (DENT and QUAD, Table 2), some selected structures (INTE, HYPO, PHAR, ANGU, and OTO) occurred in scats with no clear loss in size or loss of morphological features related to digestion. For these five structures, we ascribed the condition category good and assigned a DCF of 1.0 (i.e., no correction for partial size reduction due to digestion required).

Of the 158 structures in our blind test, 141 (89.2%) were assigned identical condition categories. Of the remaining 17 structures, 11 (65%) were noted as being borderline between categories. Angulars (ANGU) accounted for the majority (~60%) of all differences, with all but one re-assigned in good condition as opposed to fair condition. On review, differences in assigning angulars were mainly the result of differences in opinion on what constituted a well-defined and sharp point (Fig. 1, Table 1). Clarification through the additional use of reference material (including both pristine structures and examples of each condition category) is advised, particularly for angulars. Comparison of the same 158 bones between two observers (D.T. and S.H.) using the same structure reference collection resulted in assigning more than 93% (147/158) of structures to an identical category.

The regression formula for estimating pollock mass (M) from fork length (FL) estimates was best described by using an exponential equation ($M=0.0051\times FL^{3.11}$, $n=981$, $r^2=0.987$).

Discussion

The size of prey consumed by pinnipeds can usually be reliably estimated from otoliths recovered in scats if partial digestion is accounted for (Tollit et al., 1997). However, otoliths from Steller sea lion scats are often found in too few numbers, or are too digested or broken to be useful (Sinclair and Zeppelin, 2002; Tollit et al., 2004, this issue). It was, therefore, necessary to use alternative skeletal structures to estimate the size of prey selected by Steller sea lions. Zeppelin et al. (2004, this issue) documented good relationships ($r^2=0.78-0.99$) between the size of selected alternative structures and fork length for pollock and Atka mackerel. However, all skeletal structures are susceptible to digestion in the stomach (our study, and Murie and Lavigne, 1986). Thus, techniques are required to account for the degree of digestion of alternative structures prior to estimating prey size.

Reductions in the size of otoliths during passage through the digestive tract of pinnipeds have been widely reported (e.g., da Silva and Neilson, 1985; Prime and Hammond, 1987; Harvey, 1989; Tollit et al., 1997). Similarly, we found significant reduction in the sizes of all selected cranial structures from pollock and Atka mackerel. Size reduction also showed great variability. Relatively small structures were found with no obvious loss in size due to digestion, but were also frequently heavily eroded.

The degree of digestion on different otoliths and bones may be related to species, size of fish (Bowen, 2000), or even its shape, but seems to be random in any one meal (Murie and Lavigne, 1986). Degree of digestion likely depends on a range of factors such as meal size, meal frequency, meal composition, and method of consumption. In the face of these multiple factors we feel our method for classifying the degree of digestion into one of three condition categories is practical and relatively objective. However, our technique does not consider potential biases of enumeration associated with smaller prey being more susceptible to complete digestion than relatively larger prey, or of individual fish being counted more than once if all multiple structures are used. Nevertheless, resolution to these biases have been advocated (see Tollit et al., 1997; Laake et al., 2002; Tollit et al., 2003; Tollit et al., 2004, this issue). The category selections chosen with our criteria showed good agreement among independent observers.

Table 1

Distinctive external morphological features for defining the degree of digestion (condition category) as good (G), fair (F), and poor (P) for selected cranial structures of walleye pollock and Atka mackerel. Features are given in order of importance. See Table 2 for definition of structure codes and Figure 1 and 2 for illustrations. WP = walleye pollock.

Species and structure code	Category	Distinctive external morphological features
Walleye pollock		
INTE	G	1) Retains characteristic shape, notably the ridge and swan neck. 2) Both ends show no damage (except for the loss of the point and minor nicks) and do not affect length measurement.
	F	1) Ridge and swan neck clearly defined. 2) One end can show limited damage with <15% reduction. Minor nicks on opposite end acceptable, if there is no further loss in length measurement.
	P	1) Loss of characteristic shape, with ridge or swan neck (or both) ill defined. Body of structure contains holes. 2) Both ends show clear damage.
HYPO	G	1) Retains characteristic shape, with cone ~2× the length of the tube. 2) Tube end and area 1 show no damage (except for minor nicks) and do no affect the total length measurement. 3) Cone end angled when viewed from the front elevation (back elevation shown in Fig. 1).
	F	1) Tube end or area 1 shows limited damage (cone end no longer angled) clearly preventing an accurate length measurement.
	P	1) Both tube end and area 1 show damage, and a general loss of characteristic shape evident.
PHAR	G	1) Retains characteristic shape, notably a raised spout, honeycomb, and crown. 2) Crown clearly projects above honeycomb (front elevation) and is intact at area 2. 3) Clear projection of honeycomb (back elevation—see area 3). 4) No affect on measurement.
	F	1) No clear projection of honeycomb at area 3 or crown shows damage at area 2 (preventing an accurate width measurement). 2) Crown or spout (or both) can show minor damage.
	P	1) Characteristic shape lost, often only honeycomb present. 2) Honeycomb smooth, crown heavily eroded with areas 2 and 3 eroded or damaged. 3) Both ends show clear damage.
ANGU	G	1) Point sharp and well defined with no impact to measurement. 2) Area 4 in good condition and angled curve complete. 3) Neck present, but with minor damage. 4) Material of cap continues to point tip.
	F	1) Point no longer extensive or sharp or area 4 damaged and poorly defined. 2) Neck usually present, but with wear.
	P	1) Characteristic shape lost with neck often absent. 2) Point heavily eroded. 3) Area 4 shows damage or no definition.
QUAD	G	1) Groove defined from all angles and observable with the naked eye. 2) Horns rounded. 3) Angle of area 5 is clearly curvilinear. 4) Evidence of ridge and spike often observable.
	F	1) Groove unclear, forming only an indisctinct notch. 2) Horns have lost rounded definition and may be pointed or worn on one side. 3) Ridge and spike often only residual.
	P	1) Horns pointed, notch absent. 2) Ridge and spike often absent. 3) Angle of area 5 flattened. 4) Unable to determine side with assurance.
DENT	G	1) Hammerhead retains rounded end elevation features (note: both sides are not exactly symmetrical), allowing full width measurement. 2) Material in addition to the stock may be present. 3) Stock clearly curved from side elevation. 4) Width and breadth of "rounded" stock similar.
	F	1) Hammerhead shows erosion on one side, affecting full width measurement. 2) Breadth of stock reduced, but not flattened.
	P	1) Hammerhead eroded and flattened with both sides showing erosion. 2) Breadth of stock flattened, stock less rounded and less robust. 3) Unable to determine side with assurance.
OTO	P	1) Sulcus and scalloping (on most margins) well defined, and no obvious reduction in size due to digestion. 2) Able to determine side. 3) Inside strongly convex, retains characteristic shape.
	F	1) Sulcus worn but shows definition. 2) Able to determine side. 3) Scalloping worn but shows no reverse scalloping.
	P	1) Unable to determine side. 2) Scalloping worn completely smooth and reverse scalloping present. 3) Clearly broken, worn, flattened, and unable to obtain an accurate measurement.

continued

Table 1 (continued)

Species and structure code	Category	Distinctive external morphological features
Atka mackerel		
INTE	G	Like that of walleye pollock (WP) (except no point), with ridge, neck and notch clearly defined.
	F	1) Ridge present, but shows signs of wear. 2) Swan neck shows wear resulting in a "horseshoe" shape. 3) Notch shows only minor wear or chipping and does not prevent accurate measurement.
	P	1) Loss of characteristic ridge and neck with body worn (may contain holes). 2) Both neck and notch show clear damage.
HYPO	G	1) Cone rounded and complete, tube complete, retains characteristic shape. 2) Minor nicks on cone and tube may be present but do not impact total length measurement.
	F	Cone worn, loss of rounded shape, and area 1 shows minor chipping or damage or tip of tube is broken or clearly chipped.
	P	1) Cone body and area 1 show major wear, chips, and breaks. 2) Tube broken or absent entirely, unable to measure length.
ANGU	G	Like WP, additionally cap rounded and head shows only minor wear.
	F	Like WP, additionally 1) cap worn with loss of shape, 2) Head worn, chipped, and often has holes, 3) Ridge on dorsal side above neck worn smooth.
	P	Like WP, additionally 1) head shows major damage, wear, breaks, and holes, 2) Difficult to determine side with confidence.
QUAD	G	1) Horns rounded and in good condition, with angle between horns clearly curvilinear. (Note: Horns are of unequal size and shape and one side is more robust, rounded, and sloped.) 2) Evidence of ridge and spike observable. 3) Definition of left and right sides is easily achievable.
	F	1) Horns have lost rounded definition and may be pointed or worn on one side, making distinction between sides difficult. 2) Ridge and spike often only residual.
	P	Like WP, additionally no distinction between horns easily achievable.
DENT	G	Like WP (except no hammerhead), additionally 1) head retains characteristic features, tooth sockets present, 2) Ventral side of head a defined point.
	F	Like WP, additionally 1) head eroded or chipped with tooth sockets noticeably worn, 2) Point on ventral side of head eroded or chipped.
	P	Like WP, additionally head eroded or flattened with point often heavily eroded or badly chipped, accurate measurement unattainable.
OTO	G	1) Rostrum not chipped or broken. 2) Sulcus clearly defined, as are anterior and posterior colliculums. 3) Scalloping on antirostrum and posterior end clearly distinguishable. 4) No obvious wear or chipping with no obvious reduction in length (width). 5) Cristae of antirostrum forms a well-defined ridge.
	F	1) Rostrum shows some wear but remains unbroken and retains characteristic shape. 2) Sulcus still has definition despite wear, shown as a uniform channel, anterior and posterior colliculums indistinct. 3) Cristae and scalloping on antirostrum and posterior end worn smooth.
	P	1) Rostrum or posterior end broken or worn to such a degree that accurate measurement cannot be obtained. 2) Sulcus difficult to distinguish or worn smooth. 3) Cristae and scalloping on antirostrum and posterior end worn completely smooth. 4) Side cannot be easily obtained.

Nevertheless, we recommend that a hands-on reference collection be used.

The procedure we recommend to estimate fish length after classification involves excluding structures considered heavily digested (condition category poor) and applying specific condition-category DCFs (Table 2) to the remaining structure prior to calculating fish length from allometric regressions (see Tollit et al., 2004, this issue). The exclusion of structures in poor condition was necessary because of the large and variable size reduction observed in this category. Our technique uses changes noted in the morphological features of the structures themselves and is therefore not specific to Steller sea lions. Because structures are likely to erode in a predictable manner whatever the species of the stomach they are held within, it seems probable that they can also be classified into a particular condition category for use with DCFs. Consequently, our technique may be appropriate to marine piscivore dietary studies where prey size needs

Table 2

Condition-specific digestion correction factors (DCFs) for selected cranial structures of walleye pollock and Atka mackerel with associated condition categories good (G) and fair (F). Lower and upper bounds of the 95% confidence intervals (CIs) were calculated by using bootstrap resampling procedures.

Species and structure	Structure code	Grade	*n*	DCF	SD	CI	
						Lower	Upper
Walleye pollock							
Interhyal	INTE	F	54	1.1423	0.054	1.1168	1.1714
Hypobranchial 3	HYPO	F	22	1.1658	0.063	1.1343	1.1970
Pharyngobranchial 2	PHAR	F	39	1.2109	0.067	1.1717	1.2566
Angular	ANGU	F	85	1.2065	0.103	1.1670	1.2462
Quadrate	QUAD	G	20	1.2272	0.039	1.2025	1.2512
		F	27	1.2958	0.074	1.2623	1.3280
Dentary	DENT	G	17	1.1950	0.074	1.1546	1.2337
		F	31	1.3285	0.071	1.2941	1.3649
Otolith (length)	OTOL	F	37	1.1593	0.059	1.1400	1.1788
Otolith (width)	OTOW	F	49	1.2107	0.089	1.1901	1.2419
Atka mackerel							
Interhyal	INTE	F	37	1.0729	0.089	1.0374	1.1085
Hypobranchial 3	HYPO	F	23	1.1361	0.040	1.1160	1.1568
Angular	ANGU	F	40	1.1361	0.097	1.1053	1.1700
Quadrate	QUAD	G	23	1.0343	0.053	1.0070	1.0597
		F	23	1.0886	0.078	1.0551	1.1213
Dentary	DENT	G	34	1.2068	0.098	1.1666	1.2466
		F	37	1.3563	0.143	1.3063	1.4119
Otolith (length)	OTOL	F	109	1.1691	0.109	1.1459	1.1921
Otolith (width)	OTOW	F	115	1.2062	0.104	1.1837	1.2277

to be determined from partially digested prey hard remains.

Experimentally derived pollock DCFs were determined from three distinct size ranges of fish (28.5–45 cm FL), but the degree of erosion for each structure within each condition category did not show any significant differences across this range. We also found the relative shape, structure, and proportion of the morphological features used to estimate erosion were consistent for both smaller and larger fish. We therefore believe DCFs can be used for fish outside of the experimental size range of this study. Average size reduction varied between different pollock structures (12.2–24.7%) and also between condition categories, as they did for Atka mackerel (Table 2). We determined that pollock otoliths in fair condition were reduced by 14% in length, close to the 20% value estimated from reference material (Sinclair et al., 1994). Our criteria for defining a condition category of fair for pollock otoliths equates to a grade between low amounts and medium amounts of digestion as defined by Tollit et al. (1997) for Atlantic cod (which has a similar looking otolith). Our value of 14% lies midway between those determined for cod otoliths graded low and medium.

Jaw bones (DENT) were by far the largest structure used in our study but do not appear to pass through the pyloric sphincter without some level of digestion. Usually only the hammerhead and stock (representing less than a third of the whole structure) are recovered in scats. The large size accounts for the relatively greater percent mean reduction and hence higher DCF of DENT structures graded either in good or fair condition (Table 2). Although quadrates (QUAD) are also relatively large structures with a projecting ridge that is often much reduced when found in scats, we found QUAD structures of Atka mackerel recovered in scats from field studies and captive sea lion studies in relatively better condition than those of pollock, leading to differences in grading criteria and resulting DCFs (Tables 1 and 2). Part of the reason may be that the horns on a pollock QUAD project widthwise more than those of Atka mackerel, presenting a greater surface area for digestive erosion of the structural feature that is measured to estimate size (Fig. 1).

Our overall 95% confidence intervals around DCFs were generally narrow (Table 2), highlighting the tight fit of the regression formulae used and the benefits of partitioning the data into specific categories. Our bootstrap analysis suggests that resampling errors were the major source of error in calculating DCFs. Future research should concentrate on improving sample sizes for data on percentage size reduction of bones for each category, rather than on improving regression formulae. For both prey species, QUAD in good condition and OTO in fair condition, in addition to pollock INTE in fair condition and Atka mackerel HYPO in fair condition, provided the most reliable estimates of prey size (Table 2). DENT in fair condition, particularly for Atka mackerel, provided the least reliable estimate of prey size (Table 2). Measurement error was relatively insignificant, but attention should be taken when measuring ANGU and HYPO (Tollit et al., 2004, this issue).

Companion studies by Tollit et al. (2004, this issue) and Zeppelin et al. (2004, this issue) demonstrate the feasibility of applying DCFs to structures other than otoliths and the need to consider the degree of digestion to correctly estimate the length of prey eaten by pinnipeds and other piscivores. Applying appropriate digestion correction factors will lead to more refined estimates of consumption (mass of prey) by marine mammals, as well as the extent of potential overlap (length of prey) with the length of fish caught by commercial fisheries.

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