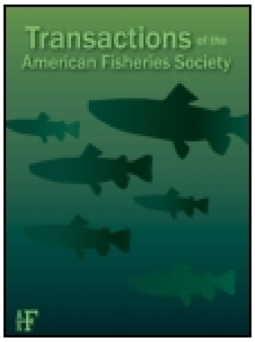

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Abstract.—We examined and measured cleithra, dentaries, opercles, and pharyngeal arches—bones found to persist during digestion of most prey fish—to identify 24 prey fish species and back-calculate their original fork length. Eighteen of the 24 species examined could be easily distinguished; however, for certain congenerics, identification was neither consistent nor reliable for all bones within the size ranges examined. Relations between bone length and fish length were linear for 14 species for which the sample sizes were adequate ($N > 30$); coefficients of determination (r^2) ranged from 0.79 to 0.99. Diagnostic characteristics and measurements of these bones provided reliable identification of genera and species and estimates of original fork lengths of partly digested prey fish from three predators. This method, compared with that of examining only prey fish in a measurable condition, greatly increased the amount of dietary information available from gut analysis.

Emphasis in the analysis of fish diets has moved away from purely descriptive studies toward the integration of food consumption rates into metabolic energetics models. When one estimates consumption rates of piscivorous fishes, several factors must be determined, including predator size and the identity, number, and original size of prey fish. Information about prey consumed must often be reconstructed from fragmentary parts. Even when the digestive process is advanced, the slower digestion of bony material and the constant relation between bone length and fish size enable reliable identification and size reconstruction for most fish.

Bones have often been used by biologists to identify otherwise unidentifiable fish and to estimate fish length and by archaeologists to reconstruct fish length and weight from remains found at archaeological sites (Casteel 1976). Bones have been used less frequently to estimate the original lengths of partly digested prey fish for feeding ecology studies (Pikhu and Pikhu 1970; Newsome 1977; Mann and Beaumont 1980). Nevertheless, vertebral columns have been used to identify fresh- and saltwater fishes and to estimate prey lengths graphically (Clothier 1950; Crossman and Casselman 1969; Pikhu and Pikhu 1970); pharyngeal arches have been used in distinguishing catostomid and other fishes during stomach analysis (Eastman 1977; Mann and Beaumont 1980); lengths of the pharyngeal arch or opercle have been used to estimate prey length by use of linear regressions (Newsome 1977; Mann and Beaumont 1980; McIntyre and Ward 1986); and pharyngeal arches, dentaries, and otoliths have been used by Eurasian biologists to estimate prey length (Popova 1967).

Our objectives are to describe the use of diagnostic characteristics of selected bones to identify prey fishes obtained from predator stomachs and to estimate original prey size from measurements of selected bones. We describe the application of these procedures in retrieving information for the estimation of consumption and the description of the food habits of three piscivorous fishes in the Columbia River.

Methods

More than 700 fish less than 250 mm long (fork length) from 24 species (Table 1) were dissected to select diagnostic bones for identification purposes and to determine the relations between the lengths of bones and fork length. The fish were collected in John Day Reservoir on the Columbia

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TABLE 1.—Species, number (N), and length of potential prey fishes collected for examination from John Day Reservoir, 1983–1986.

Family and species	Common name	N	Fork length (mm)
Clupeidae			
Alosa sapidissima	American shad	46	39–98
Salmonidae			
Oncorhynchus kisutch	Coho salmon	50	89–132
Oncorhynchus nerka	Sockeye salmon	53	78–109
Oncorhynchus tshawytscha	Chinook salmon	53	42–184
Prosopium williamsoni	Mountain whitefish	9	66–177
Salmo gairdneri	Steelhead	46	93–210
Catostomidae			
Catostomus columbianus	Bridgelip sucker	52	89–250
Catostomus macrocheilus	Largescale sucker	58	61–229
Cyprinidae			
Acrocheilus alutaceus	Chiselmouth	52	98–242
Cyprinus carpio	Common carp	3	121–147
Mylocheilus caurinus	Peamouth	40	57–194
Ptychocheilus oregonensis	Northern squawfish	50	40–238
Richardsonius balteatus	Redside shiner	34	75–120
Ictaluridae			
Ictalurus nebulosus	Brown bullhead	4	45–56
Ictalurus punctatus	Channel catfish	4	109–151
Percopsidae			
Percopsis transmontana	Sand roller	46	30–110
Cetrarchidae			
Lepomis gibbosus	Pumpkinseed	4	67–110
Lepomis macrochirus	Bluegill	7	94–132
Micropterus dolomieui	Smallmouth bass	36	34–95
Micropterus salmoides	Largemouth bass	5	120–177
Pomoxis annularis	White crappie	17	35–82
Percidae			
Perca flavescens	Yellow perch	15	84–169
Stizostedion vitreum	Walleye	13	154–233
Cottidae			
Cottus asper	Prickly sculpin	49	40–137

River or were obtained from fish hatcheries during spring and summer, 1984–1986. Specimens were immediately placed on ice until their fork lengths (± 1.0 mm) could be measured in the laboratory, and then they were frozen for later analysis. To remove bones, we thawed the fish and put them in boiling water for 30–60 s, depending on size, until the flesh could be easily removed from the intact skeleton. The bones were then preserved in 4% buffered formalin and stored in the laboratory until measured.

Identifying characteristics of the cleithra, dentaries, opercles, and pharyngeal arches were selected for examination from subsamples of 10 prey fish (or all available fish, if fewer than 10) over the size range collected. Unique characteristics of each of the bones were identified so that fishes could be distinguished at the lowest possible taxonomic level in stomach contents of predators. Criteria for comparison included shape of each bone; length of the longest axis; pattern and lengths of processes, arms, and lobes; and number or arrangement of teeth in pharyngeal bones and dentaries.

Simple linear regression equations were calculated to estimate original fork lengths of 14 fishes from nine families for which the sample sizes of bones ($N > 30$) were adequate. Fork lengths were regressed on measurements of the left bone. Bones less than 15 mm long were measured with an ocular micrometer at 8× power (± 0.16 mm), and larger bones were measured with hand calipers (± 0.05 mm) after excess moisture was blotted. Cleithra were measured diagonally, from the anteroventral tip to the posterodorsal tip (Figure 1A). Dentaries of percopsids, centrarchids, and cottids were measured from the symphysis to the posterior edge of the fork that articulates with the angular bone (Figure 2A) and dentaries of clupeids from the symphysis to the posterior edge. Salmonid dentaries were measured from the symphysis to the posterodorsal notch on the dorsal limb. Opercles of cyprinids, catostomids, percopsids, and centrarchids were measured from the anterodorsal edge to the anteroventral margin (Figure 2B). Pharyngeal arches were measured from the dorsal tip to the ventral tip (Figure 2C).

We tested slopes of regression formulas by the F-test ($P < 0.05$) to determine if they were significantly different from zero. We also calculated confidence limits (95%) and percent error (confidence limit/calculated length) through use of the shortest and longest bones in the sample to provide a measurement of error at the extreme ends of the data. We compared the total number of fish identified and sized from bones to the number of fish identified and measured by direct observations to demonstrate how the information base may be enhanced through analysis of hard tissues.

Results

Identification of Prey Fish

Diagnostic characteristics of bones used to differentiate prey fish were recognizable in the contents of predator stomachs. In general, resistance to digestion was greater for the larger, more robust bones used for identification, such as cleithra, opercles, dentaries, and pharyngeal arches. Other bones were sometimes useful in identifying fish material (e.g., fused hypurals of the prickly sculpin and preopercles of the sand roller), but these were

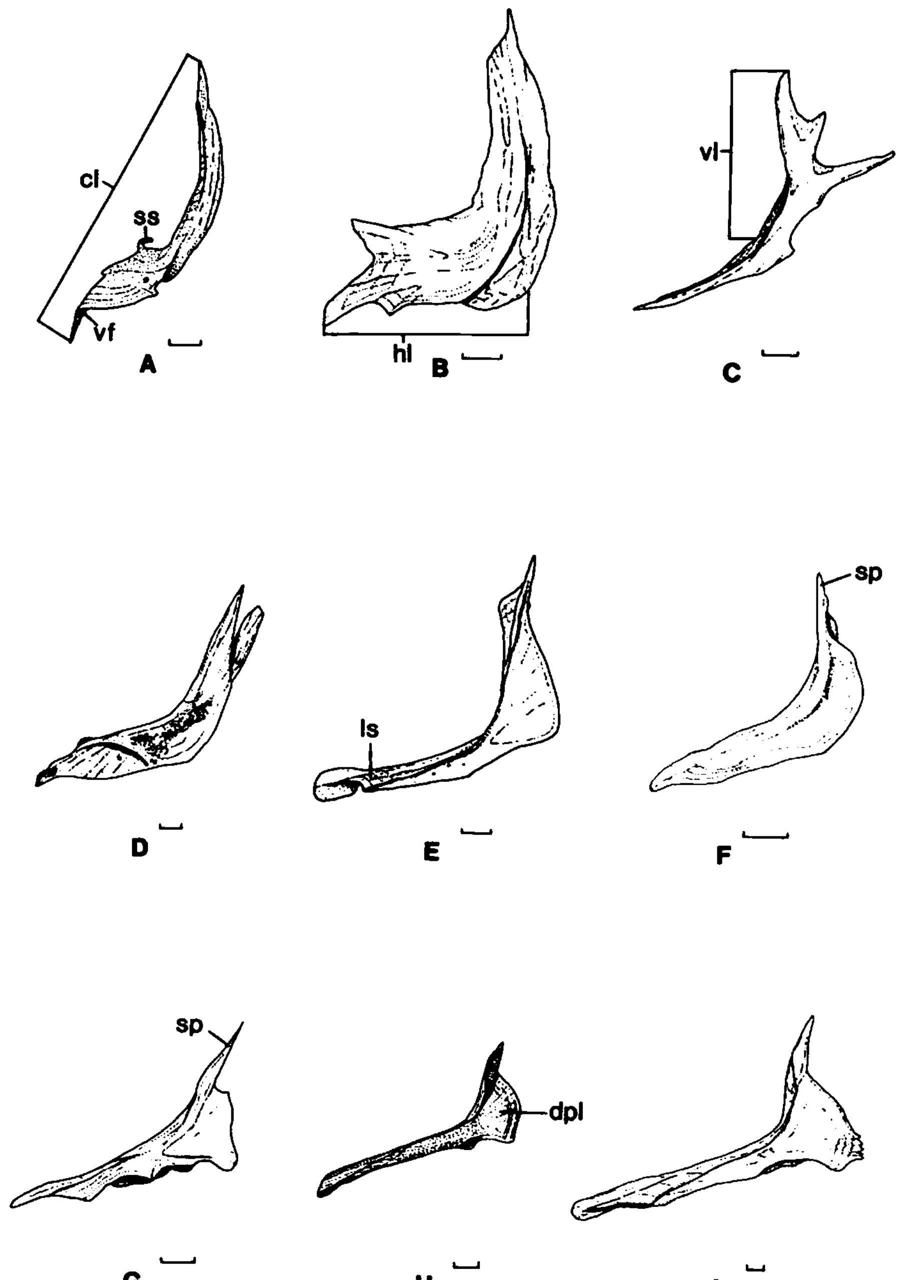

FIGURE 1.—Lateral views of left cleithra of specimens representing nine families: (A) Clupeidae, American shad; (B) Catostomidae, largescale sucker; (C) Ictaluridae, channel catfish; (D) Cottidae, prickly sculpin; (E) Cyprinidae, northern squawfish; (F) Salmonidae, chinook salmon; (G) Percopsidae, sand roller; (H) Centrarchidae, smallmouth bass; (I) Percidae, walleye. Abbreviations: cl = cleithrum length (measurement); ss = sickle-shaped process; vf = ventral fold; hl = horizontal limb; vl = vertical limb; ls = lateral shelf; sp = spine; dpl = dorsoposterior lobe. Scale bars: 2.0 mm.

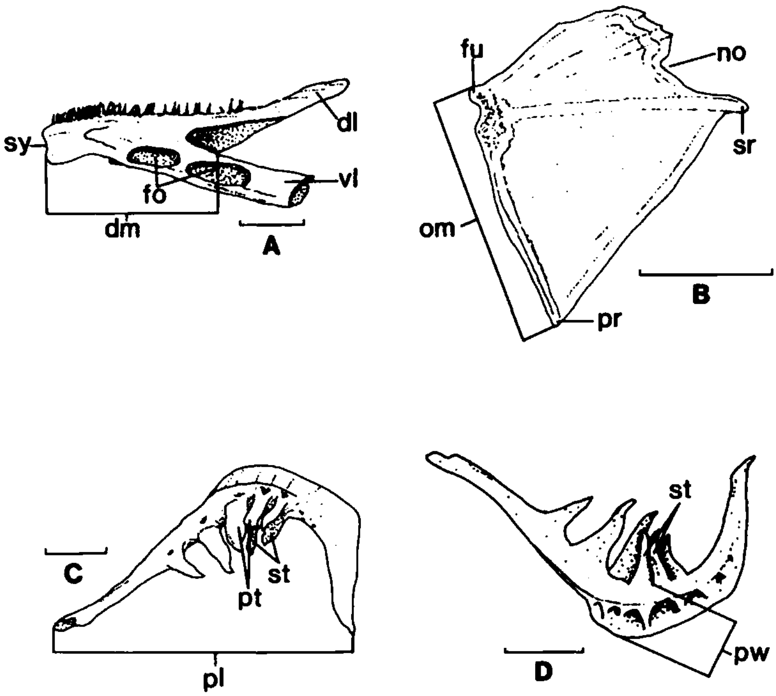

FIGURE 2.—Representative dentary, opercle, and pharyngeal arch: (A) left dentary of prickly sculpin; (B) left opercle of smallmouth bass; (C) left pharyngeal arch of northern squawfish (mesial view); (D) left pharyngeal arch of northern squawfish (dorsolateral view). Abbreviations: dl = dorsal limb; dm = dentary measurement; fo = foramen; sy = symphysis; vl = ventral limb; fu = fulcrum; no = notch; om = opercle measurement; pr = primary ray; sr = secondary ray; pl = pharyngeal arch length (measurement); pt = primary teeth; st = secondary teeth; pw = pharyngeal arch width. Scale bars: 2.0 mm.

often quickly digested and rarely were found wholly intact or in a measurable condition. Of the 24 species examined, 18 could be easily distinguished; however, for certain congenerics (*Oncorhynchus, Catostomus, Lepomis,* and *Micropterus*), identification was neither consistent nor reliable for all bones within the size ranges examined.

The cleithrum was diagnostic for all genera except those of the Salmonidae, in which steelhead could not be distinguished from the three salmon species. Other genera were separated on the basis of unique, characteristic shapes and the lengths or widths of particular features of the bone (Figure 1). In clupeids the cleithrum is fragile and has narrow limbs, a sickle-shaped process located medially, and a ventral fold (Figure 1A); in catostomids it has a horizontal limb terminating in three projections (Figure 1B); in ictalurids it has three projections on the vertical limb (Figure 1C); and in cottids (prickly sculpin) it has forked vertical limbs (Figure 1D). The cleithra of cyprinids, have horizontal limbs that terminate in an expanded lateral shelf (Figures 1E, 3), whereas those of salmonids (Figure 1F) are crescent-shaped and expanded along most of both limbs. The cleithra of percopsids (sand roller), centrarchids, and percids have similar shapes, each has a narrow horizontal limb and a spine on the apex of the vertical limb (Figure 1G, H, and I). The cleithrum of the sand roller can be distinguished from that of fish of the other families by its long spine and notched dorsoposterior lobe (Figure 1G). In centrarchids, the cleithrum has a short spine and an unnotched, dorsoposterior lobe (Figure 1H); in percids it is notched along the dorsoposterior lobe (Figure 1I).

Genera within a family can also be distinguished on the basis of the cleithra. Cleithra of the cyprinid species, for example, are distinguished on the basis of the shape and angle of the lateral shelf of the horizontal limb (Figure 3). The lateral shelf (horizontal plane or dorsal view) is slightly convex with slightly rounded corners in the redside shiner (Figure 3B); it is essentially straight, with the anterior edge angling posteriorly, in the peamouth (Figure 3C); and it is deeply emarginate in the

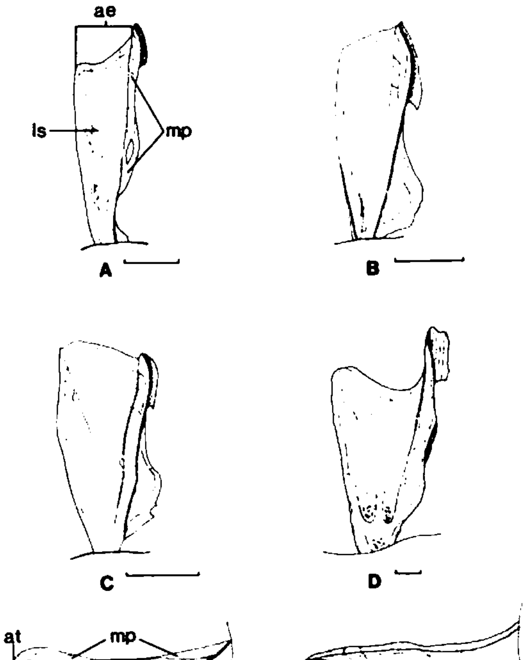

FIGURE 3.—Horizontal limbs of left cleithra of cyprinids: dorsal views for (A) northern squawfish, (B) redside shiner, (C) peamouth, and (D) common carp; lateral views for (E) northern squawfish and (F) chiselmouth. Abbreviations: ae = anterior edge of lateral shelf; ls = lateral shelf; mp = medial process; at = anterior tip of medial process. Scale bars: 2.0 mm.

common carp (Figure 3D). Cleithra of chiselmouth and northern squawfish are somewhat oblique at the anterior edge. The lateral shelf attaches at the middle of and is descendent to the medial process in northern squawfish, whereas it attaches near the top margin of the medial process in chiselmouth (Figure 3E, F).

Dentaries were diagnostic for all genera. They were rarely used for identification of cyprinids, however, because the pharyngeal arches and cleithra were much more resistant to digestion and, therefore, were recovered more frequently from stomachs. Dentaries were useful in distinguishing the three salmon species from steelhead; the dentary was wider and its ventral limb was relatively longer in the steelhead than in the salmons. Other diagnostic characters of dentaries were the general shape, presence, and distribution of teeth (e.g., single row of canine teeth in steelhead versus a cardiform pad in species of *Ictalurus*); width of the symphysis; size and distribution of foramina; number of pores (in cyprinids); and the relative length of the dorsal and ventral limbs (Figure 2A).

Opercles, though diagnostic for all families and most genera, were less resistant than other bones to digestion. These bones differed among genera in general shape and surface of margins (smooth versus serrated); in the position of the primary and secondary rays (especially in centrarchids); and in the morphology of the fulcrum, spines, and notches (Figure 2B). The opercles of cyprinids could be distinguished from those of other families but were too similar to one another to permit differentiation of genera.

Pharyngeal arches with long comb-like sets of teeth were diagnostic for the two species of *Catostomus*. Cyprinids were distinguished on the basis of the general shape of the arch and its relative width (Uyeno 1961) and on the tooth formulae for the primary and secondary (and in common carp, tertiary) rows of teeth (Figure 2C, D).

Estimates of Original Length of Prey Fish

Relations of bone length to fork length were linear and all had positive slopes that differed significantly from zero (F-test; $P < 0.01$). Regression models allowed estimates of fork lengths within ±4 mm from bones retrieved from stomachs (Tables 2, 3). From regression equations in which we used measurements of cleithra, dentaries, opercles, and pharyngeal arches of 14 species, we estimated mean fork length at the 95% confidence level with errors of less than 9, 10, 6, and 5%, respectively, at the lower end of the length ranges, and less than 2% at the upper end of the length ranges. Coefficients of determination (r^2) ranged from 0.79 to 0.99; for 75% of the regression equations, r^2 values were greater than or equal to 0.97.

Because we could not always distinguish between congeneric species by use of these bones, we used information on the relative abundance and geographic distribution of each species to aid in consumption estimates. For example, because largescale suckers contributed 92% of total suckers collected in the reservoir (Gray et al. 1985), we used the regressions developed for this species to estimate the original length of *Catostomus* spp. This procedure was followed for the other species within genera such as *Micropterus*, *Oncorhynchus*, and *Lepomis*.

Estimates of prey fish consumption by three fish piscivores in John Day Reservoir on the Columbia River from 1983 to 1986 (Poe et al. 1986) entailed the collection and analysis of stomach contents of more than 11,000 fish (Table 4). The

TABLE 2.—Regression statistics ($Y = a + bX$) relating measurements (in mm) of the cleithrum, dentary, or opercle (X) to fork length (Y) for 8–14 prey fish species from John Day Reservoir. Ranges of estimated fork length are also shown.

Species	N	Cleithrum Coefficient a	Cleithrum Coefficient b	Cleithrum Estimated length (mm)	Cleithrum r^2	Dentary Coefficient a	Dentary Coefficient b	Dentary Estimated length (mm)	Dentary r^2	Opercle Coefficient a	Opercle Coefficient b	Opercle Estimated length (mm)	Opercle r^2
American shad	42	3.94	5.67	33–87	0.98	5.60	6.93	33–87	0.98	7.22	7.99	35–98	0.98
Coho salmon	50	−17.05	9.71	46–166	0.96	6.17	11.31	52–177	0.93	9.57	12.15	53–160	0.93
Sockeye salmon	53	−14.79	9.39	76–112	0.91	−0.18	15.62	77–111	0.79	16.01	11.25	79–144	0.91
Chinook salmon	53	−15.71	9.36	19–166	0.98	−12.11	13.05	18–166	0.98	2.34	13.56	34–177	0.98
Steelhead	45	−16.70	10.27	90–201	0.97	1.71	18.18	92–917	0.90	4.44	15.64	92–192	0.94
Bridgelip sucker	52	−21.28	9.89	72–243	0.83					−20.90	12.56	76–241	0.94
Largescale sucker	58	1.10	8.06	59–198	0.99					0.15	10.65	56–197	0.99
Chiselmouth	52	−14.50	8.73	81–205	0.98					−3.84	13.92	83–209	0.99
Peamouth	40	−9.55	8.71	50–175	0.99					−2.77	13.29	55–178	0.99
Northern squawfish	50	−5.92	8.59	40–217	0.99					−1.34	13.70	39–207	0.99
Redside shiner	33	1.31	7.01	77–115	0.95					4.26	10.93	76–115	0.92
Sand roller	46	1.59	5.52	29–102	0.94	−5.06	35.08	33–93	0.89	2.62	10.09	29–106	0.93
Smallmouth bass	36	−3.59	5.97	32–87	0.98	7.42	12.59	31–88	0.97	−4.86	11.20	34–89	0.98
Prickly sculpin	49	5.08	5.47	41–134	0.99	8.43	19.53	42–13	0.98				

procedures for back-calculation of original prey lengths from bones found in stomach samples resulted in a larger volume of information on consumption estimates, depending upon the predator species. Percentages of prey fish identifiable from only bone fragments ranged from about 38% for walleyes to 92% for northern squawfish, and averaged 72% for the three predators (Table 4).

Discussion

Unique characteristics of the four diagnostic bones selected for comparison and measurement facilitated identification of prey fish species collected during our study. After some familiarization with the bones, we found that even bone fragments could be used to identify prey fish during stomach analysis, although back calculation of original lengths was not possible. Unfortunately, however, it was difficult to differentiate between certain congeneric species. Comparison of bones from smaller specimens with those from larger fish did not indicate appreciable difference in bone shape or form.

Cleithra and dentaries were more persistent in the stomach contents of predators and served as the best means of identifying prey fishes. The cleithrum, because it is relatively large and is one of the first diagnostic bones to develop, was generally the most useful bone for identifying young-of-year fishes.

We were able to identify small catostomids (<20 mm long) from the unique shape of the cleithrum. We found that the maintenance of a reference col-

TABLE 3.—Regression statistics ($Y = a + bX$) relating measurements (mm) of pharyngeal arch (X) to fork length (Y) for two species of Catostomidae and four species of Cyprinidae from John Day Reservoir. Ranges of estimated fork lengths are also shown.

Taxon	N	Coefficients a	Coefficients b	Estimated length (mm)	r^2
Catostomidae					
Bridgelip sucker	52	−25.61	17.73	81–242	0.86
Largescale sucker	58	−7.95	14.98	55–199	0.99
Cyprinidae					
Chiselmouth	52	−10.50	16.95	84–211	0.97
Peamouth	40	−1.84	14.70	51–180	0.98
Northern squawfish	49	−1.05	13.24	38–209	0.99
Redside shiner	33	−1.37	14.33	77–117	0.86

TABLE 4.—Numbers and percentages (%) of prey fish whose body lengths were estimated or actually measured during stomach analyses of three predator species collected in John Day Reservoir. The lengths of ingested prey fish were estimated by use of either diagnostic bone measurements or actual body-length measurements. Data are for 1983–1986.

Predator	Total predator stomachs	Total prey fish	Prey body length: Estimated	Prey body length: Actual
Northern squawfish	5,467	2,696	2,480 (92%)	216 (8%)
Smallmouth bass	4,940	2,894	1,887 (65%)	1,007 (35%)
Walleye	1,206	1,095	419 (38%)	676 (62%)
Total N or (%)	11,613	6,685	4,786 (72%)	1,899 (28%)

lection of bones of various sizes was useful, especially for identifying bone fragments.

The unique characteristics of pharyngeal arches have been well documented (Scott and Crossman 1973) and have been used for identification of cyprinid fishes whose opercles are easily digested and are, therefore, difficult to distinguish. Newsome (1977) encountered a similar problem in distinguishing each of the seven cyprinid prey fish he studied; therefore, he used only the pharyngeal arches for identification. Although the ability to estimate lengths of ingested fish on the basis of the dimensions of diagnostic bones varied among predator species, in our study the amount of information available from stomach analysis increased by 50–1,100%, thus reducing the number of predators required in a sample to obtain a given number of prey items. The differences in the percentages of prey fishes identified from bones retrieved from different predators may have been due to differences in several factors, such as digestibility of fish versus nonfish items, the proportion of prey fishes ingested (e.g., adult walleyes are almost exclusively piscivorous in John Day Reservoir), digestion rates, or various combinations of these factors.

The linear relations of bone length to original body lengths observed in our study differed from those reported by Newsome (1977); the latter were curvilinear between opercle and body lengths for 10 prey fish species. However, our linear relations were consistent with those of Mann and Beaumont (1980) and McIntyre and Ward (1986), who estimated body lengths by use of pharyngeal arches. McIntyre and Ward (1986) found that length estimates of fathead minnows *Pimephales promelas* based on pharyngeal arches were more accurate than estimates of lengths of 10 prey fish species based on opercles, as judged by values of coefficients of determination (Newsome 1977). In general, we obtained slightly more accurate estimates of fish length from measurements of the cleithrum and opercle than from measurements of pharyngeal arches or dentaries.

We found no instances in the literature of cleithra and dentaries being used to estimate the lengths of prey fishes found in the stomachs of piscivores. Scott (1977), however, used cleithra to estimate the length of Atlantic cod *Gadus morhua* found among remains recovered from a shipwreck, and White (1936, 1953) estimated lengths of fish by comparing measurements of maxillary, dentary, and parasphenoid bones found in regurgitated gizzard pellets of the belted kingfisher *Ceryle alcyon* with measurements of bones from specimens of known length.

Several limitations should be considered when diagnostic bones are used to estimate original lengths of ingested prey fish. The length regression equations developed in this study were from measurements on bones subjected to the effects of preservative. We recommend that, before use of these regression statistics, future investigators follow similar preservation procedures to avoid bias resulting from the potential effects of preservatives on fish bones. One should also be aware that use of diagnostic bones may bias data on food habits by favoring larger over smaller prey fish because their bones may be more resistant to digestion.

Our results suggest that the identification and measurement of cleithra, dentaries, opercles, and pharyngeal arches of prey species provide an easy and reasonably accurate method of estimating original length of prey fish in partly digested remains. This method may enable investigators to gain useful information that might otherwise be lost when prey fish lengths cannot be obtained by direct measurement.

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