



Do Digestive Processes Leave Diagnostic Traces on Fish Bones?

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This study examines the extent to which fish remains are affected by digestive processes and includes experimental and comparative analysis of tui chub (Cyprinidae: *Gila bicolor*) fish remains from modern human feeding experiments, modern coyote scats and archaeological human coprolites. Body part representation varies across the samples, but overall, bone loss resulting from digestive process is less than that documented for fish remains in previous studies. Selected elements are examined for surface modifications (pitting, rounding, adhering tissue, staining, deformation) and degree of completeness. Results show that digestive processes often modify specimens, but that many remains are unaffected. Remains that pass through human and coyote digestive tracts are similarly modified, thus distinguishing fish remains generated by the two agents is not possible using the attributes described. A sample of fish remains from western Nevada is examined for surface modification and specimen completeness to determine whether the fish remains were modified by digestive agents. Results show that at least some of the fish fauna had been ingested by mammals.

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Introduction

Over the last several decades a small but important body of research has examined how animal bones and teeth are affected by vertebrate digestive processes (e.g. Lyon, 1970; Casteel, 1971; Korth, 1979; Andrews, 1990; Schmitt & Juell, 1994; Stahl, 1996). The goal of such work has been to identify the immediate physical agent (*sensu* Gifford-Gonzalez, 1991) that generated an ancient faunal accumulation and, hopefully, the specific actor (e.g. human, bird, coyote) responsible. Such work stems from the realization that many agents can produce a faunal deposit and that before such a deposit can be used to address questions of palaeoenvironments or predator-prey relationships, in particular, human subsistence practices, the taphonomic origins of that deposit must be understood.

One obvious approach to linking a faunal accumulation to human food use would be to analyse human coprolites. While intact human coprolites are recovered in some areas, coprolites generally are rare. Thus to identify bones resulting from consumption, partial digestion, and defaecation requires examining properties of the bones themselves. Most previous work on identifying characteristics of digestive processes on skeletal elements has focused on remains of consumed terrestrial vertebrates, namely small mammal remains, with less study on fish remains. Studies that document

fish remains' condition resulting from mammalian digestion suggest that when bones are consumed they are largely destroyed. In a series of feeding experiments carried out in the U.K., Jones (1984, 1986) and Nicholson (1993) found that 85% to 100% of fish skeletal elements were destroyed by mammalian digestion. The few elements that were recovered showed significant signs of compression, rounding, acid corrosion and staining.

In an attempt to establish the taphonomic origins of fish remains from a cave site in western North America, Smith (1985) proposed several attributes he hypothesized were produced by human digestive action, including dark-stained, acid-etched bone, adhering matrix of organic-rich particles and small-size bones dominated by anatomically internal elements like vertebrae. Importantly, empirical testing of these criteria was limited to six fish remains from one coprolite (Smith, 1985). Butler (1996) examined fish remains from a single ancient human coprolite from eastern California and noticed that less than half the remains showed evidence of staining or etching and, contrary to the results of the U.K. investigators, all parts of the skeletal anatomy were represented. Undoubtedly, some of the variability in results across these studies stems from major differences in bone structure (e.g. structural density, shape) across fish groups as well as the different circumstances surrounding food processing, consumption and digestive action.

To understand better the extent to which fish bones are affected by digestive processes, and the variables that control bone survival and surface modification, we undertook the study described here. Our goal was to document the effects of digestive processes on fish remains through experiments and comparative study of specimens obtained from known contexts: We included samples produced by humans and coyotes (*Canis latrans*) to determine whether fish deposits generated by the two agents could be distinguished. Finally, we use results from this comparative study to understand better the taphonomic origins of a large fish deposit in western Nevada, U.S.A. (Butler, 1996).

Materials and Methods

Samples

Modern human. Cypriniformes is the dominant order of freshwater fishes in western North America in numbers of species and individuals. One species in the order, tui chub (Cyprinidae: *Gila bicolor*), dominates fish assemblages from western Great Basin archaeological sites, and we therefore focused the digestion experiment on this taxon. Three tui chub measuring between 66 and 85 mm standard length (SL: tip of snout to end of hypural bone) were boiled for about 5 min and then, with limited chewing, were swallowed by an adult human female. Faeces were collected for five days and were washed through 1-mm mesh screen. Remains were sorted from other recovered tissue using a dissecting microscope and stored for analysis.

Archaeological human. Fish remains from ten ancient human coprolites recovered from Hidden Cave in western Nevada (Thomas, 1985) were examined. The coprolites are from strata that have been dated to between 3600 and 3800 BP. Smith (1985) analysed the fish remains from the matrix that was excavated from the site in 1979 and 1980, but apparently did not include the coprolite samples (Wigand & Mehringer, 1985) in his review. During prior laboratory processing, the coprolites were subdivided; a subsample of the original coprolite was available for our study. We assume that the subsampling procedure did not introduce a bias against the fish remains and that those we examined are representative (in terms of surface characteristics and body part representation) of the coprolites as a whole.

Modern coyote. The tui chub population in Harney Lake, Malheur County, southeastern Oregon has experienced a series of die-offs in the last several years. We observed large numbers of chub carcasses along the shoreline during visits in the fall of 1995 and 1996. Coyotes were observed near the lake edge feeding on the carcasses and their faecal remains containing fish bones were common. A sample of these was collected and remains from four scats, which had a similar

weathered appearance, were included in our study. Scats were washed through 1-mm mesh screens and fish remains were removed and analysed.

Body part representation

After sorting fish remains from other constituents in the coprolites, we sieved them through nested 1/8 in. (3.2 mm) and 1/16 in. (1.6 mm) mesh screens to measure specimen size. Specimens recovered were identified to the finest taxon possible and assigned to skeletal element. Remains were quantified using number of identified specimens (NISP) and minimum number of elements (MNE) (Bunn, 1982), which selects the best represented section of each element and counts the number of times it occurs in a given aggregate, in this case a collection (e.g. Hidden Cave, Harney Lake coyote scat). To calculate element survivorship, the minimum animal unit (MAU; Binford, 1978) was determined for each collection, using the MNE. Element survivorships (percentage MAU) were determined by comparing the number of elements expected to the number observed (Binford, 1984; Grayson, 1988).

Surface modification and condition

Mammalian predators initially consume whole or partially complete prey with varying amounts of mastication. As summarized by Crandall & Stahl (1995), bone passing through a mammalian gastrointestinal tract is exposed to highly acidic fluids (as high as pH 2.5 in humans) in pre-pyloric and pyloric regions and the stomach. Further, gritty particles from associated foods could physically abrade bone surfaces in the stomach and the intestines. While granting that many factors control the degree of modification caused by digestive action, several researchers (Smith, 1985; Andrews, 1990; Nicholson, 1993; Schmitt & Juell, 1994) have proposed that chewing, acid corrosion and physical abrasion will modify bones and teeth in distinctive ways, causing pitting, edge rounding, vertebra deformation, crushing or compression, and breakage, and leave an organic residue on the bone surface.

In developing our analytic protocol, we closely examined the coprolite specimens for these attributes, making comparisons to undigested, modern comparative skeletal elements. We found that significant rounding and pitting were inherent to the structure of many elements (Figure 1) and that some elements were more useful than others in showing modification. Considering these issues and time constraints, we focused analysis of surface condition on six elements, choosing them because they represented different parts of the carcass, different shapes and sizes, were common in the assemblages, and because they seemed to best express some of the modification we observed. Elements included were the articular, basioccipital, ceratohyal, opercle, pharyngeal and abdominal vertebra (Figure 2).

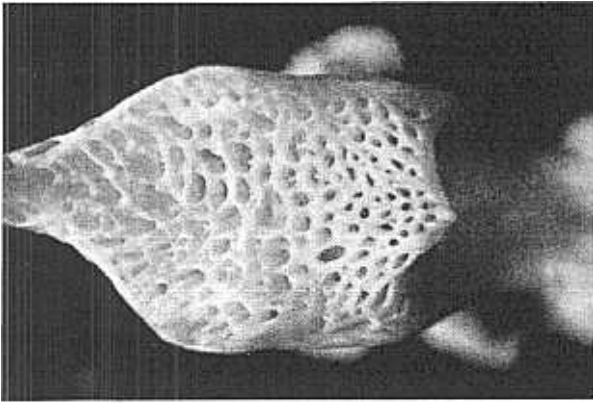


Figure 1. Close-up (12x) of basioccipital, ventral view from modern comparative skeleton. Note porous structure of unmodified specimen.

We examined the remains for the following attributes:

Pitting. Pitting refers to the presence of pits or small cavities on relatively flat surfaces of bone (Figure 3). Three of the elements, articular, ceratohyal and opercle, were examined for pitting. For the opercle and ceratohyal, pitting was recorded when multiple cavities were present that had no counterpart on modern, undigested comparative specimens. Pitting was recorded for the articular when the cavities on the antero-lateral surface were larger than on unmodified specimens. In several instances, this enlargement was in

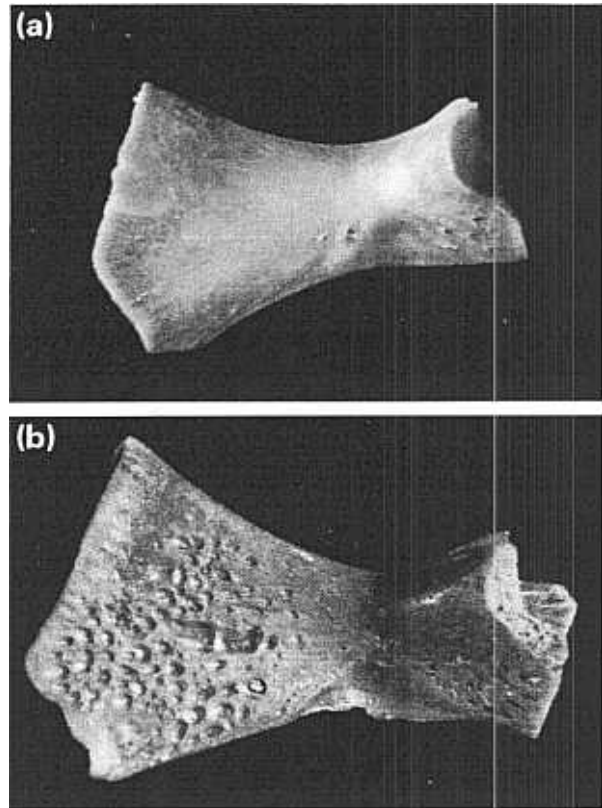


Figure 3. (a) Ceratohyal (7.5x), medial view, unmodified, modern comparative skeleton. Note smooth, uneroded surface. (b) Ceratohyal (12x), medial view, Hidden Cave (HC-449-17) coprolite specimen. Note extreme pitting.

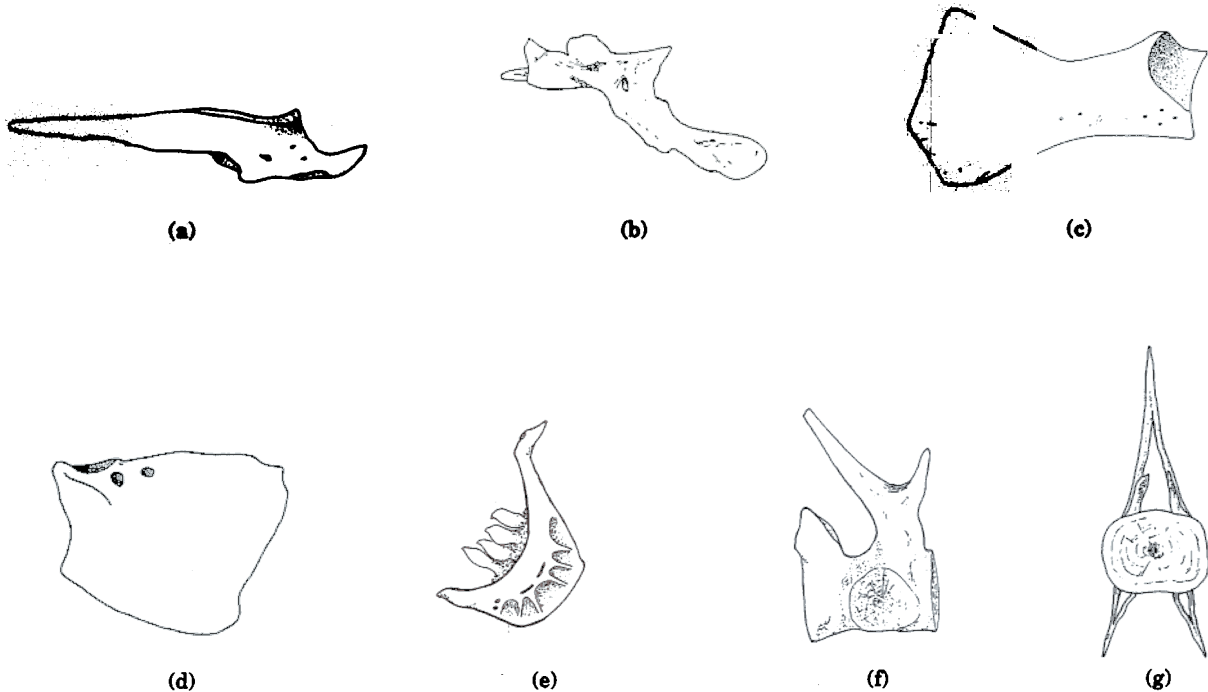


Figure 2. Elements included in the study of surface modification. Left side illustrated of paired elements. Not drawn to scale. (a) Articular, lateral; (b) basioccipital, lateral; (c) ceratohyal, medial; (d) opercle, medial; (e) pharyngeal, dorso-lateral; (f) and (g) examples of abdominal vertebrae.

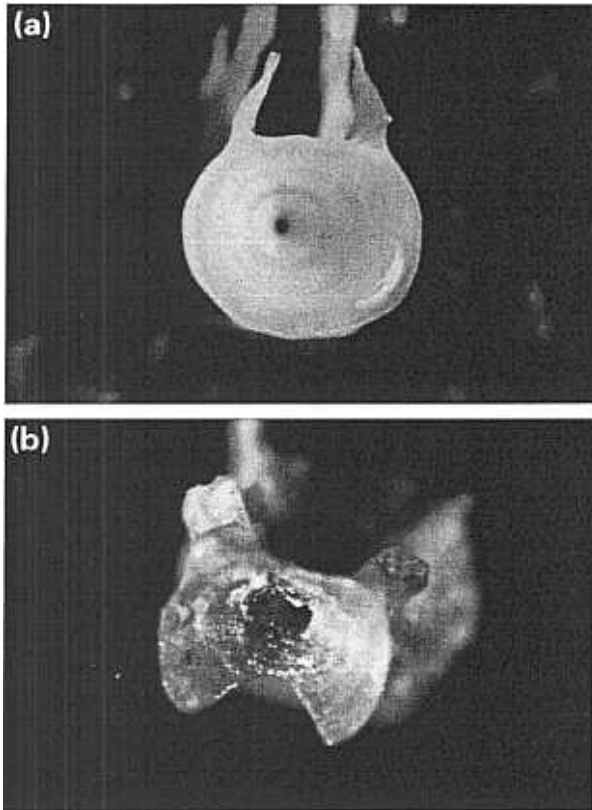


Figure 4. (a) Abdominal vertebra (11.5 ×), unmodified modern comparative skeleton. (b) Abdominal vertebra (31 ×), Hidden Cave (HC-449-14) coprolite specimen. Note scalloped, rounded edge.

the shape of a “keyhole”. Because the basioccipital and pharyngeal are naturally porous, pitting caused by digestive action *per se* would be difficult to identify; thus this attribute was not searched for on these elements. Also, we were not able to identify pitting on the complex structures of the vertebrae and thus this attribute was not recorded for this element.

Rounding. Rounding refers to the condition of broken edges or worn down original surfaces of specimens and was examined for three elements: vertebra, basioccipital and pharyngeal. On vertebrae, rounding was observed along the edges of the centrum face (Figure 4) in the form of one or more scallops or crenulations (Nicholson, 1993). On the pharyngeal, rounding was noted along the margins of broken edges. This trait is similar to pitting and we believe it is also produced by chemical dissolution of bone material during digestion. The two attributes differ in that pitting is an intrusive erosion of an otherwise relatively smooth, flat surface, or the enlarging of pre-existing cavities, while rounding is the chemical attrition of a protruding process or broken edge.

Deformation. Nicholson (1993) and Wheeler & Jones (1989) noted that digestive processes often produce vertebrae that are crushed and compressed, which they

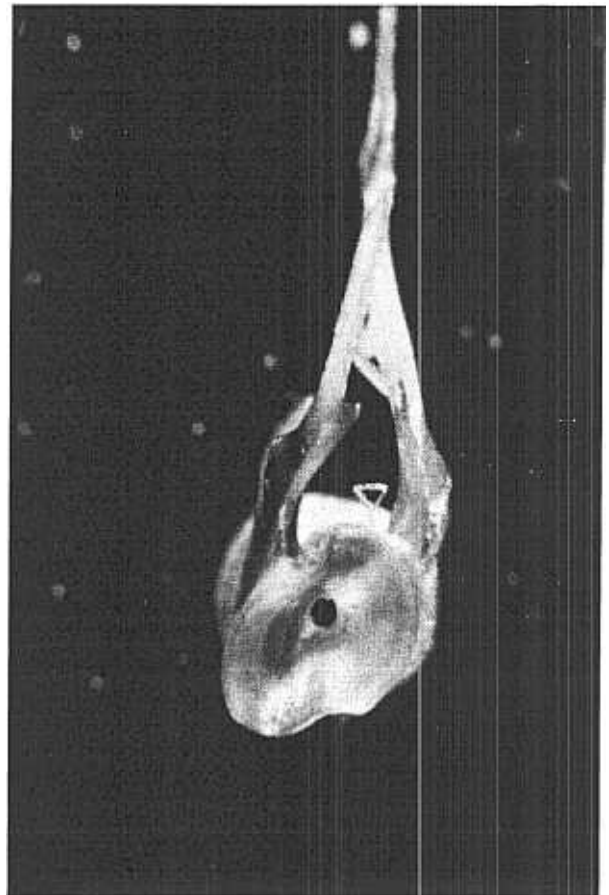


Figure 5. Abdominal vertebra (30 ×), modern human faeces. Compare to unmodified vertebra in Figure 4(a). Note deformation on this specimen.

suggest results from chewing. In our study, deformation was recorded for abdominal vertebrae that were compressed medially, dorso-ventrally or rostral-caudally or twisted along the rostral-caudal axis (Figure 5). Many of the abdominal vertebrae are somewhat flattened dorso-ventrally in modern comparative specimens. Vertebrae were considered “deformed” if they showed any alteration in shape when compared with modern comparative specimens.

Adhering organic tissue. Schmitt & Juell (1994) noted that bones from coyote scats often had organic residues (hair and viscera matting) clinging to surfaces and pits. Smith (1985) suggested that bone from coprolites had an adhering matrix of an organic-rich clay-like substance that was grey or yellow and that sometimes included bits of charcoal, hair and a variety of other organic fragments and fibres. We examined each of the six elements from the collections for signs of such residues.

Staining. Several researchers note that bone that passes through a vertebrate digestive tract becomes stained to varying degrees and suggest that intensity of staining

depends on the length of time in the gut (Schmitt & Juell, 1994) or the iron content of foods in the gut (Smith, 1985). We had difficulty assessing the presence or absence of staining on the coprolite samples. Based on Schmitt & Juell's Munsell Soil Colour Chart references, several of our modern, "undigested" comparative specimens would have been recorded as stained. Rather than treat staining as a nominal variable, we recorded some of the variation in element colour within and between the collections and review the overall potential of this attribute for taphonomic analysis below.

Element completeness. Schmitt & Juell (1994), Crandell & Stahl (1995) and Andrews (1990) suggested that element completeness or breakage patterns can vary with predator or prey body size or both. To document breakage patterns of the fish remains, bones were assigned to one of three categories based on the relative amount of element present: 0–1/3; 1/3–2/3; 2/3–complete.

The small size of the specimens necessitated microscopic analysis. Several researchers have used scanning electron microscopy (SEM) to study the effects of digestive action on bone surface morphology (e.g. Rensberger & Krentz, 1988; Wheeler & Jones, 1989; Andrews, 1990; Crandall & Stahl, 1995). The high costs associated with SEM precluded our use of this technology. Instead, we used a dissecting microscope (10–63 \times). While recognizing that some resolution may have been lost using the simpler method, we suggest that since most faunal analysts do not have ready access to SEM, descriptions based on lower power magnification may ultimately be more relevant to taphonomic research.

We acknowledge that the attributes we examined are not as yet deterministically linked to digestive processes. Not only does digestive action not always produce these modifications (see below), but agents besides digestive ones could leave similar traces. Depending on post-depositional soil conditions (e.g. availability of iron, acidity), bones can become stained (Shahack-Gross, Bar-Yosef & Weiner, 1997) or corroded and etched. Bone breakage can certainly result from post-depositional trampling or sediment compression, as well as weathering (e.g. Andrews, 1990). Recognizing this problem of equifinality and following Gifford-Gonzalez (1991), we note that in order to infer causal agency (e.g. digestive action) or actor (human versus coyote) responsible for a faunal assemblage, one needs to examine multiple, independent lines of evidence that include classes of data besides faunal remains. That said, we believe that the attributes previously described and which we document here, are potentially useful indicators of digestive action and when used in concert with other classes of information, can provide insight to the taphonomic origins of faunal accumulations.

Table 1. Frequency (NISP) of fish remains recovered by mesh size

Sample type	>1.6 mm,		<1.6 mm	Total
	>3.2 mm	<3.2 mm		
Modern human	3	59	29	91
(%)	(3)	(65)	(32)	(100)
Coyote	664	1167	57	1888
(%)	(35)	(62)	(3)	(100)
Hidden Cave	86	785	*	871
(%)	(10)	(90)		(100)
Total	753	2011	86	2850
	(26)	(71)	(3)	(100)

*Matrix not analysed.

Replication

One criticism that has been levelled against taphonomic studies of bone surface condition is the ambiguity of criteria definition or inter- and intra-analyst inconsistency in applying criteria for surface markings (Blumenshine, Marean & Capaldo, 1996). To address these problems we spent several hours examining the control collections, developing "search images" for rounding, pitting and so forth. Ultimately, Schroeder recorded the presence/absence of the attributes and estimated the completeness category for the selected elements. To estimate intra-analyst consistency in identifying the attributes, a 10% random sample of all the cases (data row in SPSS) was drawn and Schroeder reanalysed the remains. Consistency between the two analyses was extremely high (over 95%) for all the attributes, indicating minimal analyst error.

Results

A total of 2850 specimens was examined from the three collections. Based on the pharyngeal, which is species diagnostic, all of the remains from the coyote scat are from tui chub (*G. bicolor*). In the Hidden Cave sample, tui chub generated all of the 35 pharyngeals present except one (that is from *Richardsonius egregius*, another species of Cyprinidae) indicating tui chub is the dominant taxon at that site as well.

All of the remains are from very small fishes. Based on the opercle length and using the regression model in Butler (1996), body size of the Hidden Cave fish ranges between 50 and 68 mm SL (average 57 mm); coyote samples contain fish that are larger but still small, ranging between 83 mm and 156 mm SL (average 122 mm). Accordingly, the fish remains themselves are extremely small: altogether, about 70% of the remains slipped through the 3.2-mm mesh and were caught in the 1.6-mm mesh screen (Table 1).

Element representation

In a series of experiments, Jones (1984, 1986) and Nicholson (1993) fed dog, rat, pig and humans several fishes representing Clupeidae (herring), Scombridae (mackerel), Gadidae (codfishes), Lutjanidae (snappers)

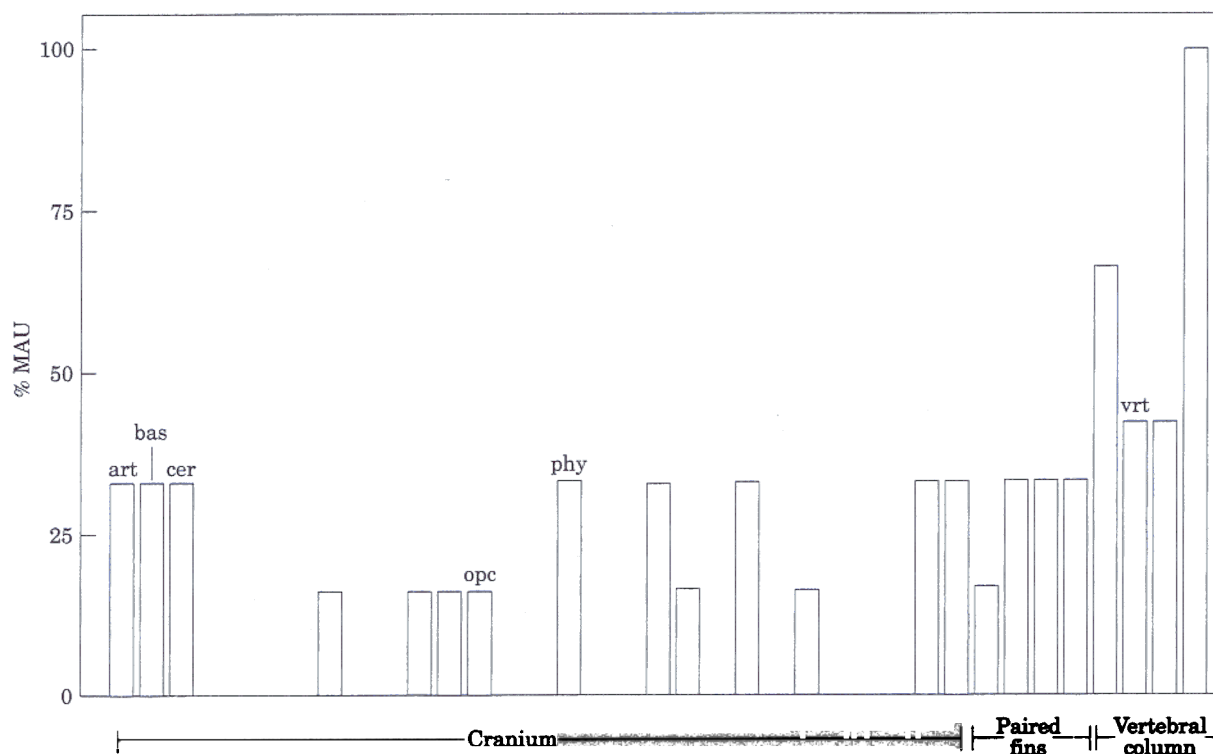


Figure 6. Element survivorship (% MAU) of tui chub remains in modern human pellet (art=articular; bas=basioccipital; cer=ceratohyal; opc=opercle; phy=pharyngeal; vrt=abdominal vertebra).

and Pleuronectiformes (flatfishes) and showed that between 85% and 100% of the elements identified from a fish skeleton were lost during the digestive process. Butler (1990) fed a dog one complete coho salmon (*Oncorhynchus kisutch*) and found only two eye lenses and one vertebra fragment in the faeces. Given the severity of destruction, Wheeler & Jones (1989) imply that evidence for human consumption of fishes will be rare (i.e. when bones are consumed) because digestive processes virtually erase the record of fish bone. In their study of the effects of human digestion on small mammal remains, Crandall & Stahl (1995) fed a human one shrew (*Blarina brevicauda*) and found similarly high attrition of skeletal elements, particularly postcranial ones. Bone loss in our human feeding experiment was not as severe as we expected from these studies and element survivorship in the ancient human coprolites and coyote scat was relatively high.

We estimated fish bone loss in the modern human sample based on counting 105 elements in a single fish. Since three fish were consumed in their entirety, a maximum of 315 elements could have been recovered in the faeces. Eighty-four elements were retained (most from the first 3 days of collection) suggesting a loss of about 74% of the original elements. To illustrate representation graphically, we also calculated element survivorship (% MAU) based on three ultimate vertebrae that provided an MAU of 3. As shown in Figure 6 and Table 2, many cranial elements were not recov-

ered, suggesting that these remains were destroyed beyond recognition during the digestive process. On the other hand, elements representing all parts of the skeleton survived to some extent, including vertebrae, paired fins, jaw and neurocranial elements.

Bone loss *per se* cannot be measured in the Hidden Cave and coyote samples because the original number of fish consumed is not known. We used element survivorship values (% MAU) to estimate element representation. When all of the Hidden Cave coprolites are treated as an aggregate, the minimum animal unit (MAU) is 17.5 (based on the pharyngeal) and element survivorships were scaled accordingly. As shown in Figure 7 and Table 2, many elements have survivorship values exceeding 50% and most values are greater than 25%. There does not appear to be any bias against particular parts of the body: high and low values are associated with each body part group (cranium, paired fins, vertebrae); vertebrae are just as common as head bones. Element survivorships were calculated for the coyote scat, treating the four samples as an aggregate. The MAU is 29, based on the ultimate vertebra. As shown in Figure 8 and Table 2, element representation is similarly high for the coyote. Vertebrae tend to have the highest representation with paired fin elements being slightly less common and cranial elements with high and low values.

The scarcity of some elements in both the Hidden Cave and coyote samples could be explained through

Table 2. Minimum number of elements (MNE) and element survivorship (%MAU) of specimens described in the study

Element	Modern human		Hidden Cave		Coyote	
	MNE	%MAU	MNE	%MAU	MNE	%MAU
Articular	2	33.3	11	31.4	44	76
Basioccipital	1	33.3	14	80	11	38
Ceratohyal	2	33.3	15	43	37	64
Dentary			18	51	40	69
Epihyal			17	48	32	55
Epiotic			5	14	15	26
Exoccipital			14	40	25	43
Frontal		16.6	25	71	32	55
Hyomandibula		16.6	15	43	43	74
Maxilla			19	54	45	77
Mesopterygoid		16.6	8	23	18	31
Metapterygoid		16.6	3	8.5	9	15
Opercle		16.6	26	74	37	64
Otolith*			11	16	32	28
Palatine			11	31	33	57
Pharyngeal	2	33.3	35	100	24	41
Parasphenoid			3	17	6	21
Prefrontal			7	20	25	43
Premaxilla	2	33.3	1	2.8	22	38
Preopercle	1	16.6	11	31.4	26	45
Prootic			4	11.4	29	50
Pterosphenoid	2	33.3	3	8.6	21	36
Pterotic			20	57	40	69
Quadrate	1	16.6	20	57	25	43
Sphenotic			3	8.5	22	38
Supraethmoid			3	8.5	11	19
Supraoccipital			12	68	10	34
Urohyal		33.3	7	40	12	41
Vomer	1	33.3	5	28	10	34
Cleithrum	1	16.6	18	51	24	41
Coracoid	2	33.3	7	20	9	15
Scapula	2	33.3	7	20	23	40
Basipterygium	2	33.3	20	57	27	47
1st, 2nd vert	4	66.7	29	83	53	91
Abdominal Vert†	24	42.1	212	32	491	89
Caudal vert†	23	42.6	125	20	361	69
Ultimate vert	3	100	15	88	29	100

*Includes asteriscus and lapillus.

†As defined in Wheeler & Jones (1989).

loss from digestive attrition or because the elements were not consumed in the first place. However, given the fish's extremely small size and the presence of all body parts (crania, fins, vertebrae), it seems likely that both humans and coyotes consumed whole individuals. Thus, we suggest that the scarcity of some elements most likely results from digestive attrition, or breakage beyond recognition.

Several researchers have demonstrated that element destruction is strongly correlated with structural bone density: the weaker the element, the more likely it will degrade. Estimates of bone density (volume density, g/cm^3 ; *sensu* Lyman, 1984) of modern skeletal elements from several vertebrates (Lyman, 1994) have been obtained that provide a valid ordinal measure of structural bone density. These values can be compared with rank order element survivorships in prehistoric faunas to determine the degree to which bone density accounts for element representation. Butler (1996) recently determined the volume density of 14 selected elements for another species in the Cypriniformes order

(*Catostomus macrocheilus*, family Catostomidae). We assume the density values for this taxon approximate those for tui chub. We would expect high and positive correlations between bone density and survivorship if differential element representation is caused by attrition, which in turn is governed by bone density.

Our expectation is met with the coyote scat, where the correlation between density and survivorship is moderately high and significant ($r_s=0.6748$, $0.02 > P > 0.01$), but the expectation was not met for the Hidden Cave remains ($r_s=0.1143$, $P > 0.50$) (Table 3). Here, several elements with low volume densities (e.g. opercle) are prominent in the collection, while elements with high densities are infrequent (e.g. "other" vertebrae). Despite the low correlation between density and survivorship for the Hidden Cave materials, we would still argue that the varying element abundance is explained by degradation and loss during digestion rather than because the elements were never consumed. Elements representing two ends of the fish (head: pharyngeal, opercle, basioccipital; tail: ultimate

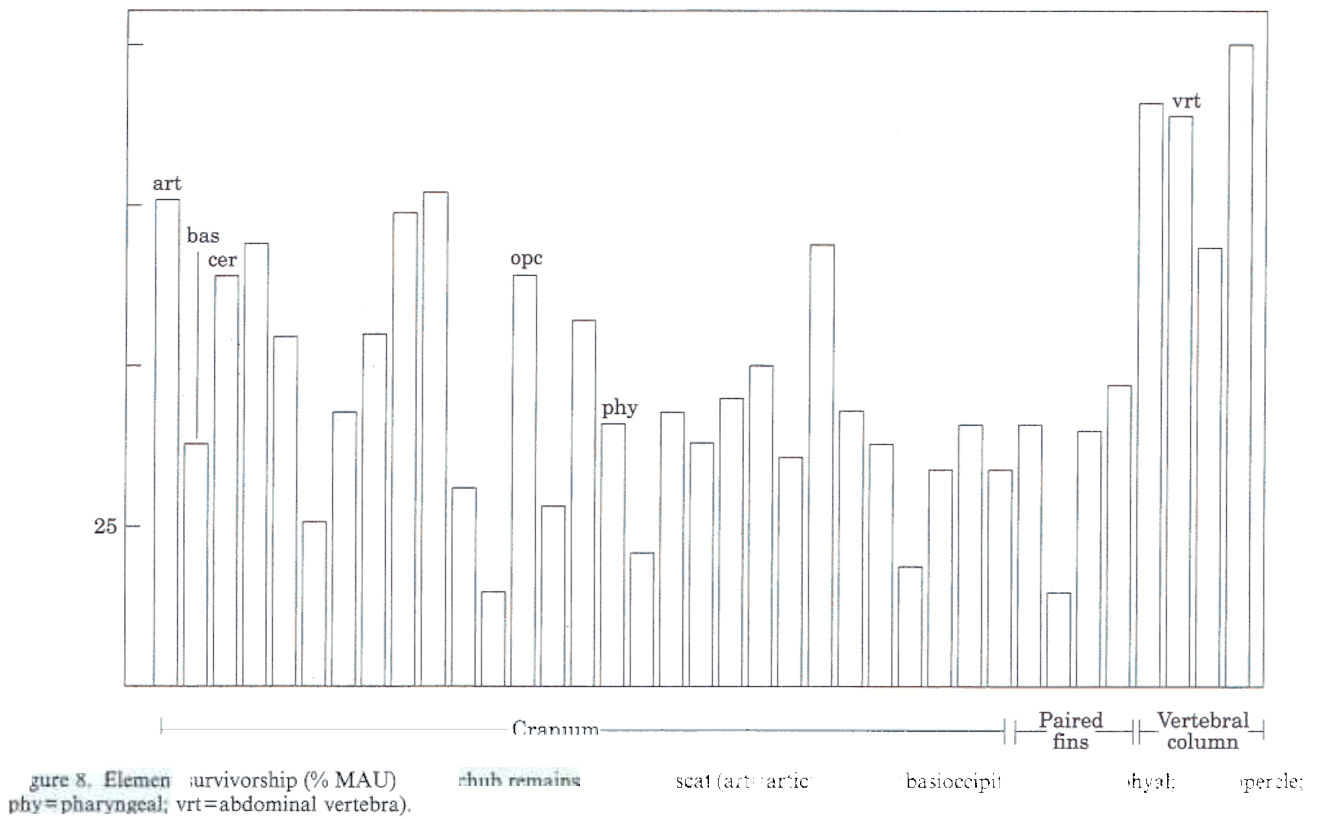
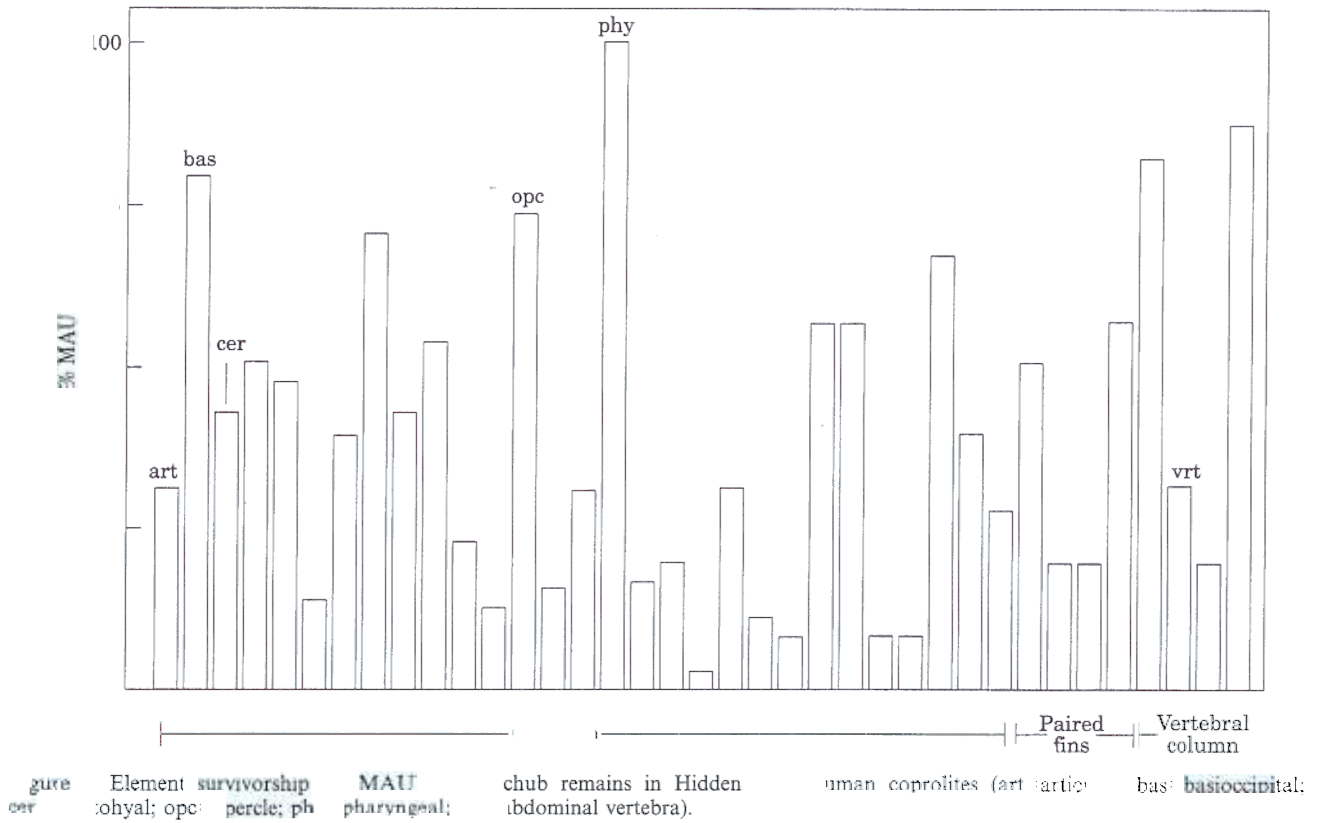


Table 3. Rank order bone mineral density (g/cm^3 ; *Catostomus macrocheilus* skeletal elements) versus element survivorship (%MAU) in the Hidden Cave coprolite and coyote scat assemblages

Element	Density		Hidden Cave		Coyote	
	g/cm^3	Rank	% MAU	Rank	% MAU	Rank
Articular	0.881	1	31	11	76	4
Dentary	0.831	2	51	8	69	5
1st, 2nd vert	0.821	3	83	2	91	1
Maxilla	0.809	4	54	6	77	3
Other vert*	0.714	5	53	7	80	2
Urohyal	0.678	7	28	12	41	10
Basipterygium	0.577	7	83	2	47	8
Pharyngeal	0.520	8	100	1	41	10
Autopterotic	0.511	9	57	5	69	5
Scapula	0.509	10	20	13	40	13
Coracoid	0.460	11	20	13	15	14
Exoccipital	0.458	12	40	10	43	9
Opercle	0.444	13	74	4	64	7
Cleithrum	0.439	14	51	8	41	10

*Includes abdominal, caudal and ultimate vertebrae.

vertebra) have similarly high survivorship (Figure 7), which strongly argues for whole fish consumption. Other properties of the elements, including shape and size as they affect identifiability (Lyman & O'Brien, 1987) for example, may help explain element representation at the cave site.

Whatever factors explain the variable frequency of skeletal elements in our study, the fact is that overall survivorship is higher in our samples than in those described by previous researchers (Jones, 1984, 1986; Nicholson, 1993; Wheeler & Jones, 1989). Part of the discrepancy could result from differences in bone density and structure across the fish groups studied. Based on visual comparison, skeletal elements of most of the fishes previously studied (the herrings, tunas and mackerels, flatfishes and cods) appear to be more porous and structurally weaker than those from the minnow (Cyprinidae) family that we studied. While we lack empirical measures of bone densities for these fishes, we can illustrate that major differences in structural bone density exist across fish orders by comparing volume densities of skeletal elements from Cypriniformes (Family Catostomidae) with those from Salmoniformes (Family Salmonidae: salmon and trouts) obtained previously (Butler & Chatters, 1994). As shown in Table 4, the Catostomidae element densities are consistently much higher (between 2 and 6 times) than those for salmonids. Such differences suggest that bone durability and preservation potential varies across fish groups. At some gross level then, the greater loss of bone in previous work could be explained by differences in bone structure and durability of the fish groups studied. As well, part of the discrepancy could relate to differences in original fish size; smaller fishes could be swallowed with less chewing and fewer bones may get broken and ultimately destroyed than bones from larger fishes (see Andrews, 1990: 28 and Schmitt & Juell, 1994:254 for a discussion of the importance of prey size and bone breakage

Table 4. Comparison of bone mineral density (g/cm^3) of taxa representing two orders of fishes

Element	Salmoniformes*	Cypriniformes†
Articular/angular	0.20	0.88
Dentary	0.19	0.83
Exoccipital	0.11	0.46
Maxilla	0.20	0.81
Opercle	0.07	0.44
Pterotic/autopterotic	0.12	0.51
Coracoid	0.07	0.46
Basipterygium	0.11	0.58
1st vertebra	0.27	0.82
Other vertebra	0.31	0.71

*See Butler & Chatters (1994), based on measuring skeletal elements of 10 chinook salmon (*Oncorhynchus tshawytscha*).

†See Butler (1996), based on measuring skeletal elements of five large-scale suckers (*Catostomus macrocheilus*).

patterns). Fishes studied previously range from 60 to 355 mm in total length (Jones, 1986; Nicholson, 1993). Although not explicitly addressed, bone loss was apparently equally severe across fish of different sizes, so at least for these studies, original prey size does not explain differences in bone survival. Other factors that could explain differences in fish bone survival include how the fish were processed before consumption as well as differences in stomach shape, kinds of foods ingested along with the fish and amount of exercise of the predator (Crandall & Stahl, 1995).

Given the small samples sizes involved and the limited research in fish taphonomy, we cannot begin to explain satisfactorily why fish bones in our modern and ancient samples fared better than those in previous experimental studies. We note that tui chub remains have been found in human coprolites in numerous other sites in the western Great Basin, suggesting that our study's results are not unique. Thus, contrary to Wheeler & Jones (1989), at least for some fish taxa in some regions, bone consumed by humans (and coyote)

Table 5. Frequency (NISP) of elements included in surface modification and specimen completeness analysis

Sample type	NISP—6 selected elements
Modern Human	28
Hidden Cave	
HC-341	32
HC-363	3
HC-372	52
HC-431	45
HC-449	116
HC-501	4
HC-656	12
HC-914	24
HC-2350	10
HC-2351	
Coyote	
Coy-2	159
Coy-3	147
Coy-4	191
Coy-9	143
Total	967

survives its passage through the digestive tract. Depending on post-depositional conditions, such remains may be present in archaeological sites, encased in coprolites or as disaggregated bony remains. Indeed, Smith (1985) argued that many of the Hidden Cave fish remains he analysed were such food remains that had passed through the human gut. Given the extremely small size of the specimens involved, to document such fish food waste in additional settings will require fine screen field recovery methods and microscopic sorting in the laboratory (Gobalet, 1989), practices that have not yet become a routine part of most archaeological research programs (James, 1997).

Surface modification and element completeness

A total of 967 specimens was examined for surface modification and degree of completeness (Table 5). Based on previous descriptions of bone from human and non-human coprolites, we anticipated that most of the remains would show modification resulting from digestive action. In fact, incidence of the traits was highly variable; many specimens showed no modification at all.

Given the small number of specimens studied from the Modern Human sample, statements about modification of the remains are tentative. As seen in Table 6, about half of the specimens that were examined show evidence of pitting, but rounding was noted on less than 5% of the analysed specimens. About 75% of the vertebrae were deformed, which Wheeler & Jones (1989) suggest is caused by chewing. Perhaps chewing can cause vertebra compression, however, the human research subject in our study swallowed the fish with minimal chewing, which suggests that deformation can occur at other stages during the digestive process (see also Crandall & Stahl 1995). Adhering tissue was

Table 6. Frequency (NISP) of tui chub remains showing surface modifications and estimates of specimen completeness from a modern human feeding experiment

Trait	Present	Absent	Total
Pitting	3	2	5
(%)	(60)	(40)	(100)
Rounding		22	23
(%)	(4)	(96)	(100)
Vert. deformation	14	5	19
(%)	(74)	(26)	(100)
Organic tissue	9	19	28
(%)	(32)	(68)	(100)
Completeness	0-33%	33-67%	67-100%
NISP	2	3	23
(%)	(7)	(11)	(82)

present on only one-third of the specimens. In terms of breakage patterns, the remains were in excellent condition; over 80% of them were at least 2/3 complete. The extent to which the specimens were stained varied considerably: some remains were extremely pale, others were quite dark in colour. Schmitt & Juell (1994) hypothesized that variation in staining of small mammal bones in coyote scats was caused by differences in the amount of time bones were in the gut. Our results support this suggestion. Specimens collected on the first day after consumption were pale (e.g. Munsell Colour Chart-10 yr 8/3, very pale brown), while specimens collected after 3-5 days were much darker (e.g. 5 yr 3/2, dark reddish brown).

To examine variation in the incidence of the attributes on the remains from human coprolites from Hidden Cave, we compared attribute frequencies across the four coprolite samples that contained at least 30 of the selected elements. As shown in Figure 9, the incidence of pitting and rounding varied considerably across samples. Pitting was very common in three of the coprolite samples, but less than half of the remains in sample HC-431 were pitted. Slightly less than half of the remains in HC-449 and HC-341 were rounded while much smaller proportions of the remains in HC-372 and HC-431 showed rounding. Intensity of staining also varied across the coprolites. For example, the remains in HC 372 and HC 341 were darkly stained (5 yr 3/3 or 3/2, dark reddish brown), while those in HC 431 and HC 914 were pale (10 yr 7/6, yellow). The coprolites were consistent in having high completeness values (most were over 2/3 complete) and minimal vertebra deformation (Figure 9). Unfortunately, for our taphonomic analysis, such consistency for these features reveals more about how little the remains were affected than about how much they were degraded during the digestive process. The only modification that was consistent across all specimens in all coprolites was the presence of organic material which was seen on every Hidden Cave specimen. This comparison shows that the extent to which remains are

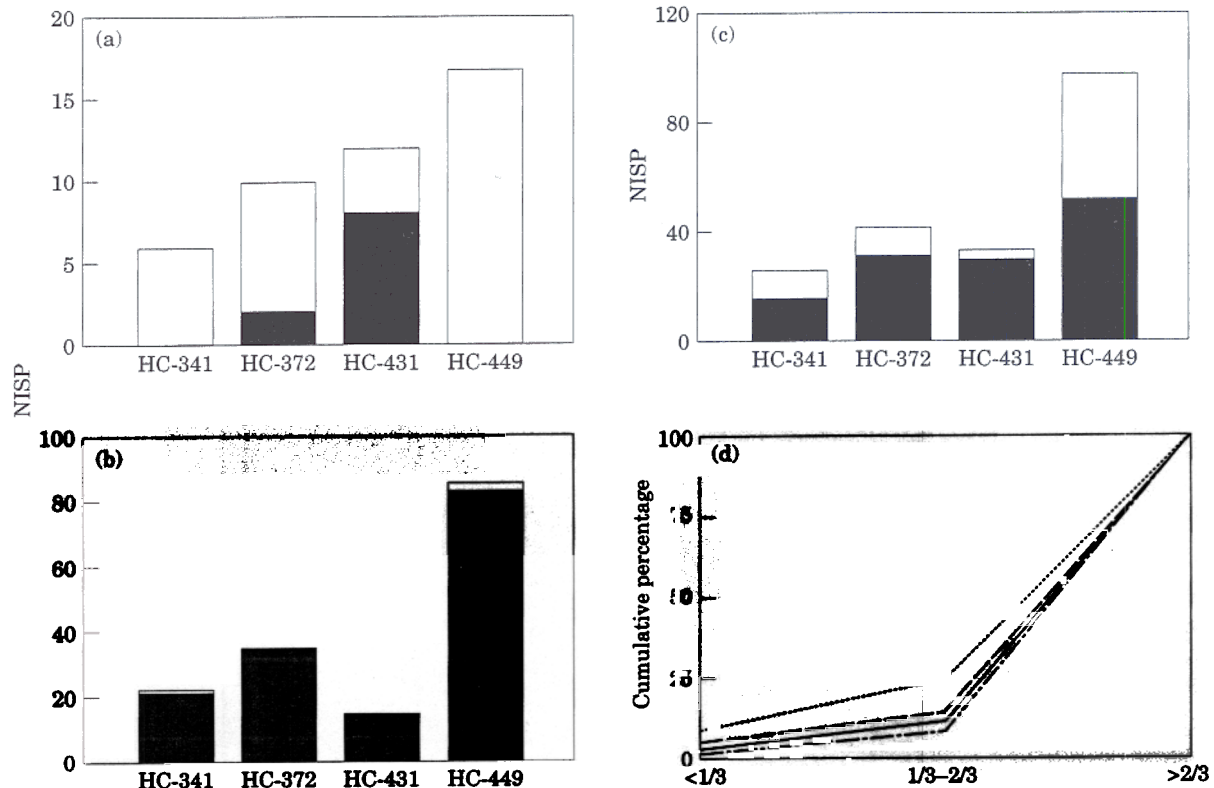


Figure 9. Surface modification and specimen completeness in four Hidden Cave coprolite samples. (a) Pitting, (b) vertebral deformation, (c) rounding, (d) completeness. □, Present; ■, absent; ···, HC-341; ---, HC-372; —, HC-431; - · - ·, HC-449.

affected by human digestive processes varies, probably for some of the same reasons that bone loss varies (see above).

Finally, for the coyote, we compared incidence of the traits and specimen completeness among the four scat samples (Figure 10). In general, the samples showed higher consistency in expression of attributes than in the Hidden Cave samples. Over half of the specimens examined for pitting in each scat showed signs of pitting, while in most samples, many fewer than half of the specimens showed rounding and deformation. Most remains were not stained but rather had a bleached, white appearance. A few specimens in Coyote-9 are very pale brown in colour (10 yr 7/4). Specimens in the interior portion of the scats had a similar bleached appearance as those exposed on the exterior of the scats, indicating that the whitened appearance did not result from bleaching from the sun. The bleached appearance of the chub remains from coyote scat is contrary to that described by Schmitt & Juell (1994) for small mammal bones in coyote scat, which they note were typically darkly stained. Adhering to each of the specimens was an off-white, greasy, clay-like material we recorded as organic tissue. Regarding element completeness, the fish remains in Coyote-4 and 9 are as complete as those in the Hidden Cave samples, whereas remains in scat samples 2 and 3 are more fragmentary (Figure 10).

Discussion

Overall, our study of surface modification shows that digestive processes often modify fish skeletal tissues, through pitting, rounding, deformation, staining, or leaving an organic residue. As such, these data may assist other researchers in their attempts to identify taphonomic agents that have generated, contributed to, or modified faunal assemblages. On the other hand these data also show that many remains can pass through both the human and non-human digestive tracts and show no sign of partial digestion. If one was to strictly use these attributes to sort out those remains which had been consumed from those that had not, many specimens would be excluded that were in fact also consumed. Thus, use of these attributes to determine whether *individual* specimens have passed through a mammalian gut is problematic at best. We suggest that these attributes are useful at identifying whether an *assemblage* of fish remains, however defined, has been modified by digestive process. Clearly, shifting the focus of the argument for taphonomic origin from the individual specimen to the scale of assemblage has problems of its own: most obviously in settings where multiple agents contributed to the deposit (and where insight to taphonomic origin of individual specimens would be most valuable). At least with regards to the modification of fish remains, given

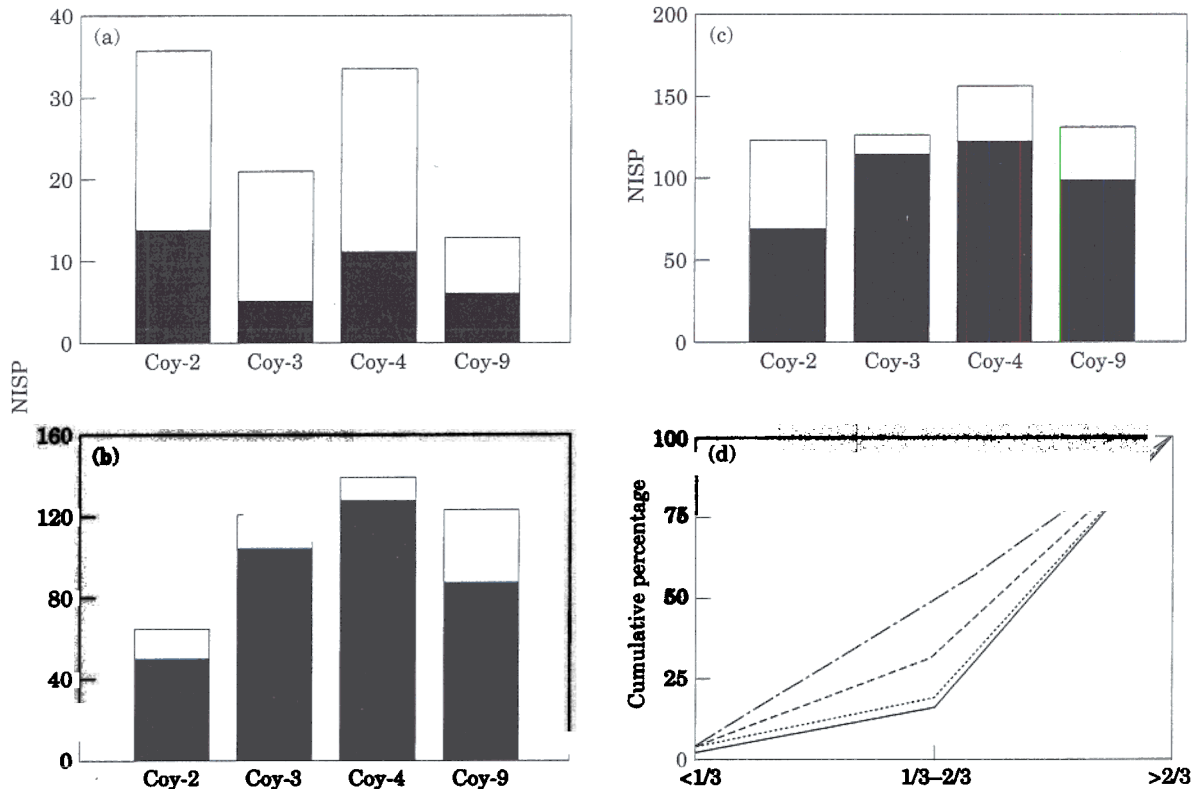


Figure 10. Surface modification and specimen completeness in coyote scat. (a) Pitting, (b) vertebral deformation, (c) rounding, (d) completeness. □, Present; ■, absent; ---, Coyote-2; -.-.-, Coyote-3; —, Coyote-4; ···, Coyote-9.

that digestive processes do not affect them in consistent ways, it is most appropriate to assess whether digestive processes have acted on a faunal sample as a whole, rather than on individual specimens.

Beyond searching for attributes of digestion, do our results show consistent differences between fish remains processed by coyotes and humans? The only consistent difference in modification patterns between the two is in bone colour, with the fish remains in the coyote sample being uniformly bleached white and the fish remains in the human samples always darker in colour. Given previous records of darkly stained small mammal remains in coyote scat (Schmitt & Juell, 1994), however, our results may not be typical. For the other attributes, the fish remains in the coyote samples tend to show a lower relative frequency of pitting and rounding and higher relative frequency of vertebra deformation than the ancient human samples. Considering the element survivorship values discussed above, fish remains in the coyote samples show overall higher survivorship than the ancient human samples, suggesting that the canid digestive process is not as destructive of fish bone. Overall, however, remains modified by coyote and human digestive process are not much different. Distinguishing fish remains generated by coyote and human digestive processes is not possible using the attributes discussed here.

The Stillwater Fish Remains: Any Sign of Digestion?

26 CH 1062, located in the Stillwater Marsh of the Lahontan Basin, western Nevada, was one of over 50 archaeological sites that was exposed by severe flooding during the mid-1980s. Site excavation and surface exposures revealed several pithouse and other features that date to between AD 600 and 1200 (Kelly, in prep.). Previous analysis (Butler, 1996) estimated that several hundred thousand faunal remains, primarily from small tui chub, were recovered from excavations. Concern that the fish remains represented a natural death assemblage (the 1980's flooding and subsequent recession produced a catastrophic die-off of fishes), prompted Butler (1996) to examine the taphonomic origin of the tui chub remains from the site. Based on reconstructed body size, fishes in the deposit were generally small (mean 89.14 mm SL) and showed a narrow size range; extremely small and large fishes were absent, which indicated a form of selective mortality. Element survivorship showed a bias against trunk elements (vertebrae) that was not expected based on natural deposition of stranded fish. Together these data suggested that cultural agents were ultimately responsible for the fish deposit.

With the results from our study on effects of digestive processes, we can ask more specific questions

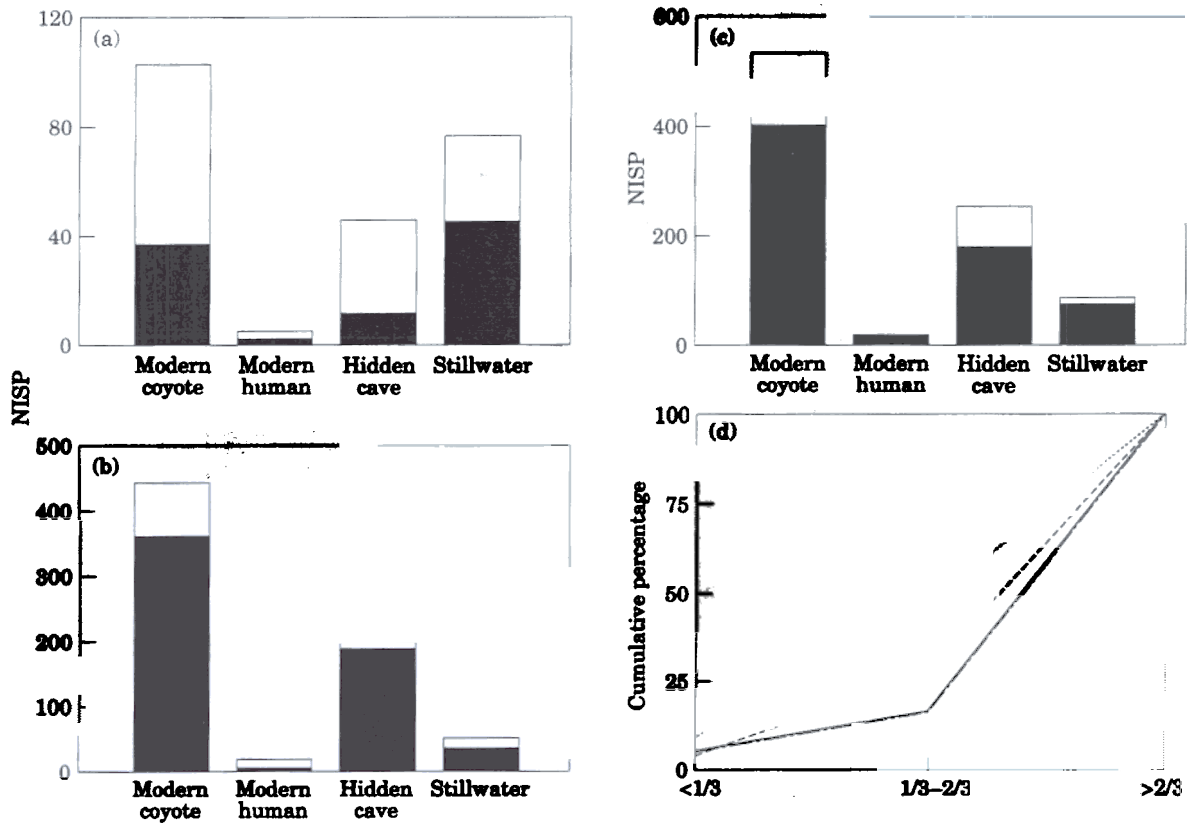


Figure 11. Surface modification and specimen completeness across control samples and Stillwater sample. (a) Pitting, (b) vertebral deformation, (c) rounding, (d) completeness. □, Present; ■, absent; --, modern coyote; —, modern human; - · - ·, Hidden Cave; · · ·, Stillwater.

about taphonomic agents that have acted on the bones. That is, do the fish remains represent individuals that were ingested by humans (or other creatures)? Given the small size of the fishes present, the most efficient way to extract their food value would have been to consume them whole. Ethnographic records from the Stillwater Marsh region (Fowler, 1992) document that small fish were often consumed whole. On the other hand, perhaps the fish remains represent fish that were caught, dried, stockpiled for later use and ultimately abandoned by prehistoric inhabitants of the site. If the first scenario is correct, we should be able to detect evidence of digestion on some of the fish remains; if the fish represent a stored resource, there should be no sign of digestive action.

To address these questions, we examined remains from a single flotation sample (Catalog No. 910) that was taken from one of the pithouse features during the 1987 excavation season (Kelly, in prep.). The sample was waterscreened using 1.6 mm mesh and all of the remains were sorted from it. We focused our analysis on the six elements of interest, using the same protocol for recording surface modification and completeness used on the control samples. A total of 170 specimens was included in the review.

None of the remains had organic tissue present that was comparable to that seen on the control samples;

given that the flotation samples were water-screened, the absence of residue may result from archaeological processing. Specimen completeness was not as high as that recorded for the control sample (Figure 11). On the other hand, a relatively high frequency of remains showed pitting (42%) and deformation (31%) and a smaller number showed rounding (15%); values similar to those recorded for both the human and coyote faecal samples (Figure 11). In addition to these modifications, the surface of 12% of the specimens possess a distinctive erosional feature, a narrow groove with a dark red stain (Figure 12), that we suspect was caused by digestive action. Since the trait was not seen on any of the specimens from the control collections, its origin remains obscure.

In short, while the sample of fish remains we examined from Stillwater is admittedly small, our results suggest that some of the Stillwater fish fauna has passed through a mammalian digestive system. Specifying whether the consumers were human is not possible. Canids used the site area during the time it was occupied, based on the presence of their remains in the 26 CH 1062 faunal assemblage (Schmitt & Sharp, 1990); remains of both coyote and dog were recovered in many sites in the Stillwater Marsh and partially disaggregated canid scats were recovered from archaeological excavations (Schmitt, 1988). Given the similarity in surface



Figure 12. Opercle (11.5 ×), right, medial view, Stillwater Flotation Sample. Note stained channel, upper right portion of specimen.

modification associated with human and coyote digestive processes, the modification could result from either human or canid activity.

Summary

Our study shows that the effects of digestive processes on fish remains is highly variable in terms of bone preservation and surface modification. Compared to other fish groups previously studied, tui chub remains (and those from related species in the Cypriniformes order) are less likely to degrade during the digestive process and thus more likely to survive as food waste than remains of other fishes. Except as identified in coprolites, however, evidence for such food waste has not been recognized in western North American archaeological sites. Whether the lack of evidence reflects a true absence in the archaeological record or coarse-grained archaeological recovery practices is not known, and cannot be established without more fine-screen sampling of deposits and microscopic analysis. Our work supports other studies of surface modification caused by digestive action that show erosional pitting and rounding, for example, on bone surfaces. Descriptions and illustrations of modified surfaces provided here should assist future researchers in identifying whether faunal remains have been modified by digestive processes. We emphasize however, that remains are differentially affected by the process and that some fish remains retain little evidence of their passage through the gut.

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