TUI CHUB TAPHONOMY AND THE IMPORTANCE OF MARSH RESOURCES IN THE WESTERN GREAT BASIN OF NORTH AMERICA

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Debates about the importance of marsh resources to prehistoric human subsistence in the western Great Basin are longstanding. Recent questions regarding the natural vs.cultural origin of fish remains in lakeside archaeological sites further impede understanding of ancient subsistence patterns. Taphonomic study of a huge assemblage of tui chub (Gila bicolor) remains from an archaeological site in Stillwater Marsh, western Nevada, was undertaken to identify agents of deposition in marsh settings. The Stillwater fish remains showed limited surface modification—cut marks, burning, and digestive etching and staining—and thus these attributes were not useful indicators of origin. Fish mortality profiles, reconstructed by regression analysis of body size, indicates cultural selection of young/small fish rather than natural catastrophic mass death. The low survivorship of vertebrae in the chub assemblage suggests differential treatment of cranial and postcranial body parts by cultural agents. The Stillwater site fish assemblage represents a vast number of small fish; the presence of small tui chub from archaeological sites throughout the western Great Basin suggests that prehistoric fishers targeted relatively small chub in the subsistence quest.

Desde hace mucho tiempo han habido debates acerca de la importancia de los recursos de las zonas pantanosas para la subsistencia prehistórica humana en la Gran Cuenca occidental de los Estados Unidos. Las preguntas recientes referentes al origen natural versus cultural de los restos de pescado en sitios arqueológicos en las orillas de lagos obstaculizan, aún más, la comprensión de antiguas pautas de subsistencia. Se emprendió un estudio tafonómico de grandes colecciones de los restos de cachos (Gila bicolor) de un sitio arqueológico en Stillwater Marsh, en el oeste de Nevada, con el propósito de identificar los agentes de sedimento en los sitios pantanosos. Los restos de pescado de Stillwater permitieron observar limitadas modificaciones de las superficies—cortes, quemaduras, el grabado digestivo y manchas—y, por eso, estos atributos no fueron indicadores útiles del origen. Las esiadísticas reconstruidas de la mortalidad de los peces utilizando el análisis regresivo del tamaño del cuerpo indican una selección cultural de los peces pequeños/jóvenes más bien que una muerte natural masiva catastrófica. El bajo índice de supervivencia de vértebra de los cachos (Gila bicolor) sugiere un tratamiento diferencial de las partes craneales y poscraneales del cuerpo por los agentes culturales. La colección de la pesquería de Stillwater representa un número enorme de peces pequeños; la presencia de pequeños cachos tui de sitios arqueológicos por todo la Gran Cuenca occidental sugiere que los pescadores prehistóricos estaban más interesados en los cachos relativamente pequeños para su sustento.

The importance of marsh resources and their relation to hunter-gatherer mobility strategies in the western Great Basin have been the subject of continuing debate for over 60 years (e.g., Aikens and Greenspan 1988; Bettinger 1993; Heizer and Kreiger 1956; Heizer and Napton 1970; Kelly 1985, 1990; Livingston 1988a, 1991; Loud and Harrington 1929; Madsen 1988; Raven and Elston 1988, 1991; Raymond and Parks 1990; Rhode 1987, 1990; Thomas 1985, 1990). In its basic form, this debate centers on the relative value of marsh versus upland resources and considers whether wetland resources could have supported sedentary or near-sedentary populations. Some researchers have emphasized the richness of wetland resources (e.g., fishes, plants, birds) and suggested that lacustrine systems could support residential bases for much or all of the year (e.g. Livingston 1991; Madsen 1979, 1988; but see Binford 1983). Others challenge this view, believing that marsh resources are not capable of supporting year-round residence and that they would be used primarily as a backup resource or when upland resources were diminished (e.g., Kelly 1985).

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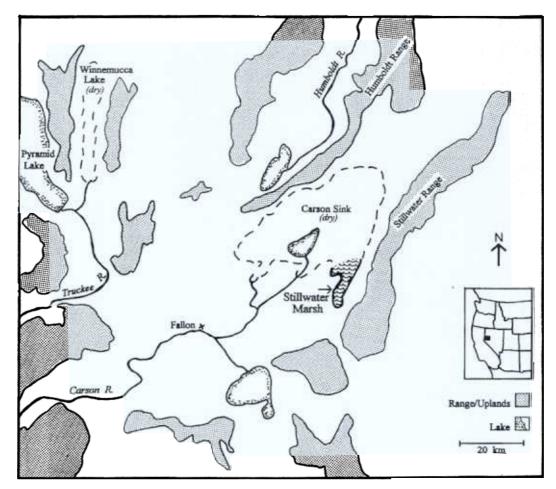


Figure 1. Map of Carson Desert, western Nevada, showing location of Stillwater Marsh.

Until recently, archaeological data available to evaluate questions of hunter-gatherer mobility strategies and subsistence components have been limited. Most of the empirical record was drawn from cave sites and, as Thomas (1985:28) has noted, these were excavated long before research focused on ecology and prehistoric lifeways. Detailed information on subsistence, seasonality of site use, and mobility strategies has been difficult to extract from site records and excavated materials obtained from field techniques driven by questions of culture history (see Livingston 1988a for an important exception).

Several large-scale regional surveys and excavations in the western Great Basin over the past 15 years (e.g., Aikens et al. 1982; Beck 1984; Bettinger 1975; G. T. Jones 1984; Kelly 1985;

Rhode 1987; Thomas 1985) have advanced our understanding of prehistoric land use in marsh and upland environments (Bettinger 1993). However, documenting the role of particular food resources in prehistoric subsistence has been hampered by nagging taphonomic questions about the origins of faunal materials in marsh and adjacent cave sites (e.g., Greenspan 1988; Livingston 1988a; Smith 1985). Recent events in the Carson Sink of western Nevada (Figure 1) illustrate this condition. The archaeological record from the Carson Sink underwent a dramatic transformation resulting from extensive flooding of the basin during 1982-1984. Subsiding floodwaters exposed numerous pithouse features, burials, and dense artifact scatters and provided, at least for some researchers, compelling evidence for intensive

and residential use of the marsh for multiple seasons, if not the entire year (Raven and Elston 1991; Raymond and Parks 1990).

Exposure of the Stillwater Marsh sites has bolstered the view that wetlands could support residential bases during some periods in the past. However, specific understanding of the nature of marsh resource use based on faunal remains has been difficult given taphonomic concerns. Concern over the origin of the fish remains, which represent between 20 and 85 percent of the faunal remains in marsh sites, has been acute (e.g., Greenspan 1988; Raven and Schmitt 1991). As Raven and Schmitt (1991:56–57) recently lament "the role of fish in human subsistence remains poorly understood as most bones are complete, unburned, and show no evidence of partial digestion."

Such concern over fish bone origin is certainly reasonable. Indeed, the same floods that exposed the Stillwater archaeological sites suggest processes that might have naturally deposited fish carcasses in such locales in the past. The exceptionally high water flows into the Carson Sink in the early 1980s led to the tremendous population explosion of tui chub (Gila bicolor) (Rowe and Hoffman 1987), the dominant fish taxon in marsh archaeological sites. Beginning in 1985, lake levels began to decline; water ceased flowing into the basin while evaporation continued, resulting in decreased water levels and high salinities. In January 1987, the lake froze, which probably raised salinities beneath the ice. During the winter of 1987, an estimated 7 million fish carcasses, primarily from tui chub, were found along 40 miles of the Carson Sink shoreline. Apparently the fish reached maximum salt-toleration levels and perished (Rowe and Hoffman 1987).

Water levels in the Carson Sink have fluctuated in the past (Benson and Thompson 1987; Morrison 1964); tui chub populations have undoubtedly experienced boom-bust cycles as well. It is not unlikely that bony remains resulting from carcasses stranded along lakeshores have become incorporated into lacustrine archaeological sites (Greenspan 1988; Raven and Schmitt 1991).

The Stillwater Marsh archaeological record clearly holds promise for modeling the evolution

of hunter-gatherer mobility strategies and prehistoric land use (Kelly 1988; Raven and Elston 1988; Raymond and Parks 1990). However, in order to incorporate the faunal record into those models, we must devise ways of distinguishing between bone deposited by natural and by cultural processes (e.g., Schmitt 1988a). Here, I draw on recent analysis of fish remains from one of the Stillwater sites (26CH1062) to assess the potential contribution of natural death and deposition to the Stillwater fish bone deposit. I evaluate multiple lines of evidence, including fish mortality patterns, bone surface modification, and body part representation to argue that a human agency is primarily responsible for the deposit. I then discuss the implications of these findings to our understanding of fish resource use in the western Great Basin.

The Site: 26CH1062

26CH1062 is located in the Stillwater Marsh, one of a few existing wetlands situated on the floor of Pleistocene Lake Lahontan in the western Great Basin (Figure 1). Stillwater Marsh lies at 1,180 m asl in the Carson Desert of western Nevada, one of the lowest points in the region. The largest basin in the western Great Basin, the Carson Sink is a wide, flat valley characterized by sand dunes, alkali flats, and slightly alkaline marshes (Kelly 1988). The desert receives water from the Carson River, which drains the eastern side of the Sierra Nevada Range in California, and, periodically, water from the Humboldt River, which drains mountain ranges in east-central and northeastern Nevada. Rainfall averages 123 mm/year.

Abundant research on the Pleistocene-Holocene geomorphic history of the Carson Sink documents the dynamic nature of the drainage systems, water level, and wetland distribution over the past 13,000 years (e.g., Benson and Thompson 1987; Davis 1982; Morrison 1964; Russell 1885). The earliest archaeological record from Stillwater dates to between 4,950 and 3,300 B.P. (Elston et al. 1988). Elston et al. (1988) suggest that, during the past 5,000 years, the Stillwater region probably contained transitory shallow ponds, lakes, and marshes created by blowouts and dunes, which formed dams trapping water.

Table Frequency of Fish Remains.

Taxon	NISP
Cyprinidae	5,259
Gila bicolor	956
Gila bicolor cf. obesus	229
Gila bicolor cf. pectinifer	37
Catostomidae	208
Catostomus tahoensis	51
Cyprinidae/Catostomidae	2,270
Total	9,010

Notes: Samples were from 26CH1062; 3.2-mm mesh was used. NISP = number of identified specimens.

26CH1062 is one of over 50 archaeological sites in the marsh area exposed by severe flooding from 1982 to 1986. Intermountain Research (Silver City, Nevada) undertook test excavations at five of the sites (Raven and Elston 1988). Robert Kelly directed excavation at a sixth site, 26CH1062, which provided the fish remains I analyzed and describe here. Together these sites represent occupations dating between 3,200 and 650 B.P., based on projectile point types and radiocarbon dates (Raven and Elston 1988). All of the sites are characterized by variably shaped depressions, including some probable pithouses (Raven and Elston 1988). Faunal analyses have been conducted by Dansie (1987), Greenspan (1988), Livingston (1988b), and Schmitt (1988b).

26CH1062 is composed of five to six pithouse features and numerous smaller features. Excavated matrix was water-screened through 3.2-mm mesh. Residue from 18 flotation samples, which included all material retrieved in 1.6-mm mesh, also was available for analysis.

Preliminary sampling and analysis of the 3.2mm screened matrix estimated over 290,000 fish remains in the excavated sample and the presence of only two species, tui chub (*Gila bicolor*) and Tahoe sucker (*Catostomus tahoensis*). Most of the remains were from tui chub. To obtain a representative sample of this voluminous assemblage, I drew a 50 percent random sample of all excavation unitlevel bags; from each selected bag, 100 specimens were drawn. To ensure adequate representation of pithouse features, three unit-level bags from two of the pithouse features were completely analyzed. Given the similarities in taxonomic and body part frequencies between these two samples, the results presented here are based on the combined samples. As shown in Table 1, 9,010 specimens representing two species of fish were identified in the 3.2-mm samples from 26CH1062. Most of the specimens that could be identified to family are cyprinid; tui chub is the only species of this family present. The remains in the Cyprinidae/Catostomidae category include fragmentary or eroded materials that could not be assigned to family or vertebrae that are difficult to distinguish between families.

To determine whether use of 3.2-mm mesh biased taxonomic recovery. I scanned six of the flotation samples with a low-power microscope. I was particularly concerned to know whether extremely small cyprinid species (e.g., Richardsonius egregius and Rhinichthys osculus) might be present only in the fine-screen sample and thus focused analyses on pharyngeals (toothed branchial arches found in the back of the mouth), which are readily identified to species. Of the 114 pharyngeals identified in the flotation samples, only 4 (3.5 percent) represent speckled dace (Rhinichthys osculus), whereas the rest are from tui chub. Thus, even if all the sediments had been screened with 1.6-mm mesh, tui chub would still be the dominant fish taxon represented. Consequently, taphonomic and subsistence issues discussed below focus on this taxon.

Fish Mortality Patterns

Numerous workers have used age/size class profiles reconstructed from archaeological and paleontological faunas to identify exploitation strategies and to determine whether deposits represent a cultural or natural origin (e.g., Frison 1978; Hoffecker et al. 1991; Klein and Cruz-Uribe 1984; Lyman 1991; Noe-Nygaard 1983; Speth 1983; Stiner 1991). Two theoretical models of population structure have been defined for fossil populations. A population structure that resembles a typical living population, wherein successively older age classes contain progressively fewer individuals, has a catastrophic age profile. Natural agents (i.e., flash floods, volcanism, and epidemic diseases) and cultural procurement strategies (i.e., bison traps) may produce a population structure with a catastrophic age profile. Reconstructed fossil populations in which prime age adults are underrepresented and young

and old individuals are relatively more abundant have attritional age profiles. Natural causes for this population structure are starvation, accidents, predation, and disease-factors that affect the most vulnerable members of the population, the young and the old. Cultural procurement may also exploit the most vulnerable members of the population through either capture of living individuals or scavenging of deceased animals that perished from other attritional factors.

In the context of this study, I suggest that the population structure of a natural death assemblage of tui chub would have a catastrophic profile. All age/size classes would be affected by shrinking lake levels and rising salinities. Tui chub in three age classes died during the winter 1986-1987 at Stillwater Marsh and their carcasses were found together along the shoreline (Rowe and Hoffman 1987). Furthermore, because the youngest/smallest members of the population are the most abundant, members of such classes should be the most abundant in the fossil assemblage. The mortality pattern should reflect that of the overall population age/size structure. (It is possible that some tui chub age cohorts are more likely to die from elevated salinities or reduced water or oxygen levels than others. If this is the case, then the fossil population structure would vary from the catastrophic profile described. Unfortunately, little is known about tui chub physiology or developmental changes in physiology to evaluate this possibility. Ideally, the theoretical catastrophic profile of a natural tui chub death assemblage could be compared to an empirical one, generated from a study of the recent fish kill at Stillwater. However, information required to create such a profile [e.g., length frequencies, ages] was not collected.)

On the other hand, cultural procurement-use of nets, spears, hook and line, and other techniques-may select particular size classes of the population. For example, the kind of net used and its mesh size can greatly affect the body size of the catch (Cailliet et al. 1986; Hamley 1975 and references therein). Impounding nets (e.g., seines), usually set around particular fish aggregations from shore or boat, trap all fish larger than the mesh size opening of the net; fish smaller than the opening swim through. Entangling nets

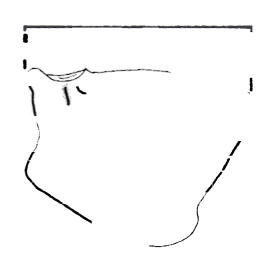


Figure 2. Tui chub opercle (left side, medial view), showing portion measured (OL). (For scale, this length ranged between about 4 and 24 mm on the modern specimens.)

(e.g., gill nets), set out for a specific period and then retrieved, select a much narrower size range. These nets catch fish that enter the mesh opening beyond their gill covers but cannot pass completely through; the fish cannot back out of the net because the mesh is caught behind their gill covers. Fish smaller than the mesh opening easily swim through; fish larger than the mesh opening cannot penetrate deeply enough into the mesh to be entangled (Hamley 1975).

Thus, the population structure of a culturally generated assemblage may be different from that produced by natural catastrophe. The age/size distribution of the cultural assemblage may be unimodel or multimodal depending on the kind and number of techniques used.

The fossil population structure of the 26CH1062 fish deposit was estimated by using

reconstructed fish body size, which is highly correlated with fish age at least in the first several years of life (e.g., Moyle and Cech 1982). To estimate body sizes of the prehistoric tui chub at 26CH1062, it was first necessary to determine the relation between bone size and body size. I chose the opercle (the primary element of the gill cover) for the regression analysis because it is one of the most abundant elements in the prehistoric assemblage and because the element is easy to remove from modern carcasses.

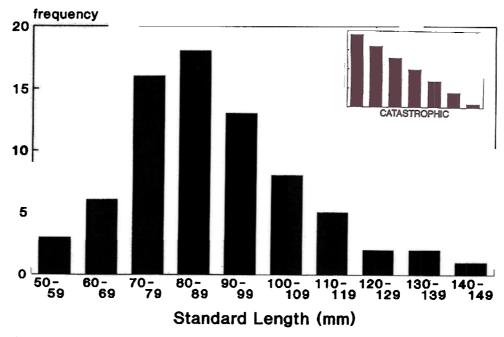


Figure 3. Reconstructed tui chub length frequencies (SL) from 26CH1062; inset illustrates catastrophic mortality profile.

Based on a modern sample of tui chub (n = 143) collected from several locations in western Nevada, I performed regression analysis (Casteel 1976:95) using the variables opercle length (OL) (maximum length of anterior border of the opercle bone) and standard length (SL) (end of snout to end of hypural bone) (Figure 2). The exponential model was most appropriate ($r^2 = .985$), providing the regression formula (natural logarithms):

$$\log SL = 2.51260 + .90851(\log OL)$$

I then measured the OL of the 74 archaeological cyprinid specimens with the anterior border intact. Although most of these opercles probably are from tui chub, the element can be identified to family only on the basis of morphological criteria. Some of the opercles may be from speckled dace, given that dace was identified in the flotation samples and based on the extremely small reconstructed body sizes of the archaeological fish (see below). This analytic difficulty should not introduce much error into body size reconstructions, however, given the overwhelming predominance of tui chub in the assemblage. In addition, morphological similarity in opercles across family members suggests that the regression model should hold for other species in the family.

Using the regression equation obtained from the modern sample, I then calculated predicted standard lengths of the prehistoric fish. As shown in Figure 3, the reconstructed length frequencies of the fossil population are normally distributed with a mean of 89.14 mm (s = 18.60), ranging between 52.27 and 142.69 mm SL. As compared to the inset in Figure 3, the fossil population structure bears no resemblance to a catastrophic profile. Extremely small fish (<50 mm SL) and medium to large fish (>150 mm SL) are absent entirely.

How do these data correspond to growth and life history characteristics of tui chub? Chub may reach 20–40 mm SL in their first few months of life and grow to lengths of 350 mm SL (Carlander 1969:394), living to be over 30 years old (Scoppettone 1988). The modern sample of Stillwater tui chub used in the regression analysis ranged from about 50 to 210 mm SL.

Whereas more detailed life history information has not been gathered for Stillwater Marsh fish, a recent age and growth study of tui chub in Eagle Lake, another relatively shallow water lake in the Lahontan system of northeastern California, provides some insights on the prehistoric sample from Stillwater. From seven gill net and minnow seine sets during June and July 1986, Davis (1986) recovered over 800 tui chub, ranging in size from less than 20 mm to over 350 mm SL. He estimated the age of the individuals by counting annuli (growth rings) on the opercle (Scoppetone 1988) and calculated the mean body size (SL) by age class (Table 2). Thus, fish of 22 mm SL were recently hatched young of the year, those of 91 mm SL had hatched the previous summer and were in the 1+ age class, chub with lengths of 141 mm were in the 2+ age class, and so forth (Table 2).

If we can assume that the chub growth patterns for Eagle Lake and Stillwater Marsh are similar, then the body size data from the Stillwater archaeological sample suggests that fish primarily died toward the end of their first and during their second year. Fish representing the 0+ and 3+ age groups and older are absent.¹

If the 26CH1062 fish assemblage resulted primarily from natural mass death, we would expect a much larger number of smaller young of the year and more of the larger individuals. The small mean body size and unimodal distribution of sizes suggests some selective mechanism of procurement. However, two analytic biases may affect the size of the fossil opercle measured and thus the reconstructed body sizes of the fossil population: screen mesh size used and differential breakage mediated by size.

Biases

Opercles of extremely small fish could have been lost through the 3.2-mm mesh screen used during excavation. To examine the potential for such loss, I retrieved and measured opercles from eight of the flotation samples that were screened with 1.6-mm mesh. The size class distribution in the 1.6-mm mesh sample differs somewhat from that in the 3.2-mm sample (Figure 4). Mean fish size in the 1.6-mm fraction (75.65 mm, s = 14.53) is slightly, albeit significantly, smaller than the mean body size in the larger mesh (89.14 mm SL, s = 18.61) ($t = 2.95 > t_{.05(2),87} = 1.98$). Although I cannot exclude the possibility that opercles of extremely small fish slipped through the 1.6-mm mesh, such loss seems unlikely.² This comparison

Table 2. Tui Chub (Gila bicolor) mean SL (mm) b	y age
class, Eagle Lake, California (Davis 1986)	

Age ^a	Mean Size	S.D .
0+	22.1	± 2.32
1+	91.5	± 6.48
2 +	141.4	± 14.3
3 +	177.6	± 20.0
4 +	212.8	± 22.6
10 +	341	

⁸Age class 5 + through 9 + not captured.

Table 3. Estimated Size of Tui Chub Opercles.

OL (mm)	SL ^a (mm)	Incomplete MNE (%)	Complete MNE (%)
		62 (14.8)	
		288 (68.6)	
		63 (15.0)	
		6 (1.4)	
		• 1 (.2)	
		420 (100)	

^aBased on regression formula (natural logarithms), log SL = 2.51260 + .90851 (log OL).

suggests that the use of 3.2-mm mesh has introduced slight bias to the reconstructed body size distribution in the direction of larger fish.

It is possible that opercles of smaller, younger tui chub are less sturdy and thus might suffer higher attrition and fragmentation from destructive processes than opercles from larger chub.³ If larger or smaller opercles tend to be broken with greater than random frequency, then the sample of measured opercles may not adequately reflect the fossil body size distribution. Over 700 cyprinid opercles were identified from the 26CH1062 sample, whereas only 10 percent of these were complete enough to measure and include in the size class reconstructions. To examine the potential for bias introduced by differential breakage, I estimated original opercle size of the broken specimens as follows. I selected five opercles from the modern tui chub sample with opercle lengths measuring 5, 10, 15, 20, and 25 mm. Each of the broken fossil opercles were then compared to the opercles of known size and placed in the most appropriate size class category. For example, fossil opercles closest in size to the 5-mm opercle were placed in the OL category, 2.5-7.5 mm; fossil opercles closest to the 10-mm opercle in size were placed in the 7.5-mm to 12.5-mm OL cate-

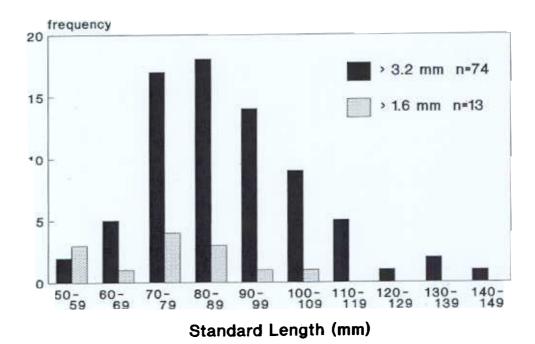


Figure 4. Comparison of reconstructed tui chub length frequencies represented in 3.2-mm mesh fraction and 1.6-mm mesh fraction 26CH1062.

gory, and so forth. Over 400 of the fossil opercles were complete enough to assign to such size class categories (Table 3).

The frequency distribution of estimated body size (Figure 3) is somewhat affected by bone breakage, with larger specimens showing a greater tendency to be incomplete than smaller ones (Table 3). Over 32 percent of the complete, measurable opercles are in the smallest size class, whereas only about 14 percent of the incomplete specimens are from this class. About 17 percent of the incomplete specimens are from fish larger than 122 mm, whereas only about 5 percent of the complete, measurable opercles are from fish this large. Thus, the low frequencies of larger fish in Figure 3 in part may reflect the fact that only complete opercles were used to generate that graph. Sizedependent breakage, however, does not explain the low frequencies of the smaller fish.

Screen mesh size and size-mediated breakage have affected the body size reconstructions to some extent. Use of 3.2-mm mesh biases body size in the direction of slightly larger fish, and differential breakage biases body size reconstruction in the direction of smaller fish. Neither of these biases, however, challenges the basic structure of the tui chub mortality profile. The scarcity of younger fishes and the relatively narrow size range does not suggest catastrophic mass or nonselective death but rather indicates a form of selective mortality.

Surface Modification

Whether bone has been burned, bears cut marks, and shows sign of digestion are other commonly used indicators of depositional origin (e.g., Balme 1980; Greenspan 1988; Lyman 1982; McGuire 1980; Richter 1986; Schmitt and Sharp 1990; Shipman et al. 1984; Smith 1985). Although burned bone in an archaeological site can result from natural fires (e.g., forest, grass fires), if multiple artifact classes and sediments do not show evidence of burning, it is reasonable to assume that cultural agents are responsible for the burned bone. However, even if cultural agents are responsible for the fire that burned bone, one would still need to consider the possibility that cultural burning postdates the natural deposition of fish remains.

Widespread burning is not indicated at 26CH1062. Thus, presumably, humans are responsible for the fires, which in turn burned faunal materials. Of the 9,010 fish remains from

the site, 120 (1.3 percent) are burned. Relatively more postcranial elements and fewer cranial elements are burned than expected by chance events (Table 4; chi-square = 26.59, p = .0000), which may reflect differential processing of body parts. On the other hand, even if differential burning across body parts reflects cultural processing per se, such practices were not common, given the small proportion of burned specimens. Burning does not provide compelling evidence for cultural origins of the fish remains.

Cut marks, which would provide direct evidence for cultural processing, were not identified on any fish specimens. It is not known whether the absence of such marks results from limited butchering, limited contact of tools with bone, breakage tendencies of the bones themselves, or the fact that human agency was not involved in bone deposition.

Evidence for human ingestion of fish carcasses including the bones also has been used to infer cultural origin of fish remains in the western Great Basin (Greenspan 1988; Raven and Schmitt 1991; Smith 1985). Archaeological evidence that prehistoric inhabitants of the western Great Basin consumed whole or partial tui chub comes from bones found in human coprolites (Follet 1967; Roust 1967) and chub remains inferred to be from coprolites based on digestive etching and other attributes (Smith 1985). Based on his analysis of fish remains from Hidden Cave, Smith (1985:173) described several attributes indicating ingestion, digestion, and defecation: dark-stained. acid-etched bone; adhering matrix of organic-rich substance that sometimes included bits of charcoal, hair, and other fibers; bones of uniformly small size; and overrepresentation of internal bones (e.g., vertebrae, pharyngeal teeth, and basioccipitals). Smith does not indicate whether these attributes are specific to human coprolites or whether fish remains from coprolites of nonhuman predators and scavengers could have similar attributes.

Smith's criteria may characterize some fish bones that have passed through the digestive tract of a human or some other vertebrate. However, my recent analysis of fish bones recovered from a single human coprolite excavated by Robert Bettinger from Fish Slough Cave (Owens Valley,

Table 4. Frequency of Burned Specimens across Body Parts, 26CH1062

	Burned		Not I	Burned
Body Part	Obs	Exp	Obs	Ехр
Cranial	36	64.5	4,805	4,776.5
Postcranial ^a	84	55.5	4,085	4,113.5

"Elements posterior to basicccipital, including pectoral and pelvic fin elements (chi-square = 26.59, p = .0000)

California) suggests that Smith's criteria do not apply to all coprolite bone. The Fish Slough Cave fish remains, representing the Cyprinidae and Catostomidae families, were examined by lowpower magnification. Of a total of 87 fish specimens in the coprolite, only 40 (46 percent) are stained dark red. None of the specimens shows digestive etching. Given the small sample size, my results obviously are tentative, but they point out the difficulty of using Smith's criteria to determine whether digestive processes affected fish remains.⁴

The 26CH1062 fish specimens do not exhibit any of the attributes that Smith describes. None of the fish remains are stained or acid-etched nor were organic-rich materials adhering to any of the bony specimens. Although the fish remains are relatively small, representing fish averaging about 90 mm SL, this small size simply indicates that such fish *could* have been consumed whole and not that they *were*.

Raven and Schmitt (1991) suggest that the lack of evidence of staining and digestive etching on most of the Stillwater fish remains indicates that the fish were not ingested by humans, which in turn calls into question the cultural origin of the bones. As noted above, however, fish bone that passes through the human digestive tract does not necessarily become stained or etched. I suggest that the variables controlling staining and acid-etching are more complex than previously conceived. Thus, for the present, the absence of staining and acid-etching cannot be called upon to argue for a natural origin of the Stillwater fish remains.

Body Part Frequency

Body part frequency is commonly used to identify the agent(s) responsible for a particular fossil assemblage (e.g., Binford 1981; Binford and Bertram 1977; Brain 1981; Stiner 1991). Such studies generally assume that different agents (e.g., birds, humans, water) modify or destroy particular classes of elements in distinctive ways. Although Lyman (1984, 1985) and Grayson (1988) have cogently argued that the structural density (g/cm^3) of bones is the ultimate cause of element destruction in most contexts, proximate causes may vary considerably across depositional contexts because of differences in the ways taphonomic agents procure and process carcasses.

I assume that while bone density plays a critical role in structuring fossil fish assemblages, there should still be non-density-mediated differences in element representation between natural and cultural tui chub deposits because of major differences in the nature of the agents generating the deposits (Lyman 1984). Carcasses resulting from natural mass death were presumably deposited whole along the shoreline as the water level declined. Such events were observed by biologists working at Stillwater after the recent tui chub population crash (Rowe and Hoffman 1987:Figure 10). Although scavenger birds and mammals no doubt assisted in the breakdown of fish carcasses and modified and destroyed bones, in situ weathering was probably the main destructive agent. In these natural settings, the absence of a dominant taphonomic agent focusing on soft tissue anatomy should result in higher correlations between density and survivorship (Lyman 1984).

In cultural settings, human processing and consumption of fish carcasses should significantly affect element representation (Butler 1993). For example, ethnographic records of fish processing in the Great Basin (Fowler 1986:88, 1992:63) indicate that fish were often preserved by drying; both fresh and dried fish were further prepared by boiling or roasting in the ashes of the fireplace (Fowler 1992:63; Kelly 1932:97). Dried fish often were pulverized and added to other dishes (Fowler 1986:88). At Stillwater Marsh, larger fish (Tahoe sucker and large tui chub) were dried on racks; although they were split lengthwise to promote drying, they were not filleted (Fowler 1992:63). At Pyramid Lake, only the fillets obtained from cui ui (Chasmistes cujus) were preserved (Fowler 1986; Stewart 1941).

Human consumption of whole or parts of fish may also affect element representation. The ethnographic record for Stillwater inhabitants, suggests that

small fish (usually dried) were boiled whole in soups.... Their bones softened and they could be eaten whole if they had not disintegrated during boiling.... Small fresh fish were baked in the ashes in packets made by placing them between two layers of cattail leaves This process kept the fish clean and also softened the bones so they could be eaten along with the meat. [Fowler 1992:63]

As mentioned above, the presence of tui chub bones in prehistoric coprolites indicates that some fish were consumed along with their bones. Based on analyses of 30 human coprolites from Lovelock Cave, Follet (1967) identified 474 tui chub pharyngeals representing a minimum of 298 fish. Follet suggests that the fish represented in these coprolites come from fish 38 to 139 mm long, although he does not describe how such size estimates were made. He also argues that the well-preserved condition of the pharyngeals reflects that at least the heads of these fish had been eaten whole. Because pharyngeals alone were identified, the Lovelock data do not provide any estimates on overall element survivorship in coprolites. Follet's report does provide clear evidence that at least some parts, the head including the bones, of small tui chub were consumed.

With a few exceptions (Fowler 1986), ethnographic accounts do not specify whether heads and trunks were treated differently during processing. Previous work on salmonid taphonomy suggests that differences in the distribution of meat and bones between the head and trunk in part structured the way these body parts were butchered and cooked, which in turn affected element survivorship of the two body parts (Butler 1993).

If the Stillwater fish fauna results from natural death and deposition, element survivorship should show a high correlation to bone density given the absence of a dominant taphonomic agent (e.g., humans) focused on soft tissue anatomy. If the fish fauna was generated primarily by cultural agents, element survivorship should show a much lower correlation to bone density given the variety of intervening factors, including cooking, butchering, consumption, and disposal, which may affect bones of the head and trunk in variable ways.

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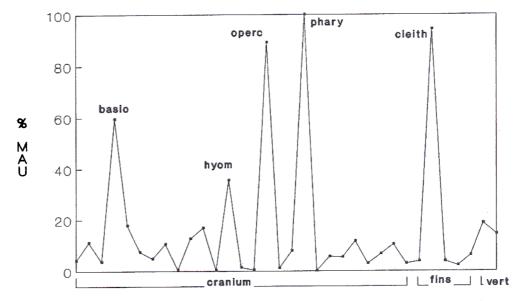


Figure 5. Element survivorship (percent MAU) of Cyprinformes remains, 26CH1062 (basio, basioccipital; hyom, hyomandibula; operc, opercle; phary, pharyngeal; cleith, cleithrum).

Of course, chub assemblages originally produced by cultural or natural agents could be modified further by water sorting. Discrete elements or articulated parts could be moved away from the original site of deposition. The floodwaters of the 1980s that exposed the Stillwater archaeological sites probably moved materials found in those sites (Dansie 1987), and past flooding episodes could have sorted exposed bone accumulations. Such transport would affect element representation and potentially obscure the distinctions described above. Controlled flume studies and field observations of mammal bone transport by water (Behrensmeyer 1975; Voorhies 1969) and field observations of natural fish bone accumulations on lakeshores exposed to differing amounts of wave action (Stewart 1991) suggest that water effectively sorts bones by their density, size, and shape. For example, Stewart's (1991) study of modern natural fish bone accumulations on the shore of Lake Turkana, Africa, found that collection locales exposed to the greatest wave activity had a disproportionately high number of dense elements. In the context of this study, a high correlation between bone density and element survivorship could just as easily reflect natural death and deposition (no aqueous transport) as cultural use and deposition (followed by water sorting).

Interpretations of the bone density-element survivorship relationships discussed below will bear these issues in mind.

Element survivorships for the 26CH1062 assemblage are based on identifiable remains from both the cyprinid and catostomid families of the Cypriniformes order. Because most of the vertebrae could not be identified to family, the more inclusive taxonomic category had to be used in order for the postcranial elements to be included in analysis. Given that over 96 percent of the assemblage is cyprinid, and virtually all of these remains are from tui chub, body part frequencies presented here primarily reflect that of tui chub.

Element survivorships were determined by first calculating the minimum animal unit (MAU, Binford 1978); when the entire site was treated as an aggregate, the fish remains provided a MAU of 520, based on the pharyngeal. I based MAU calculations on the 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 (Grayson 1988). The MNE for vertebrae were based on the presence of 50 percent or more of the centrum. Element survivorships (percent MAU) were calculated by comparing the number of elements expected relative to the number observed

Table 5. Frequency (MNE) and Survivorship (Percent MAU) of Cypriniformes Skeletal Elements, 26CH1062

Element	MNE	%MÁU
Cranium		
Articular	43	4.13
Autopterotic	115	11.06
Autosphenotic	37	3.55
Basioccipital	309	59.42
Ceratohyal	185	17.79
Dentary	78	7.50
Entopterygoid	51	4.90
Epihyal	110	10.58
Epiotic	5	.48
Exoccipital	132	12.69
Frontal	175	16.83
Glossohyal	1	.19
Hyomandibula	369	35.48
Maxilla	14	1.34
Metapterygoid	5	.48
Opercle	927	89.13
Palatine	12	1.15
Parasphenoid	41	7.88
Pharyngeal	1,040	100.00
Premaxilla	1	.09
Preopercle	58	5.58
Prootic	55	5.29
Quadrate	120	11.54
Supraethmoid	15	2.88
Supraoccipital	34	6.54
Urohyal	54	10.38
Vomer	15	2.88
Fins		
Coracoid	39	3.75
Cleithrum	980	94.23
Scapula	39	3.75
Supracleithrum	22	2.11
Basipterygium	63	6.06
Vertebrae		
First vertebra	97	18.65
Other vertebra	2,522	14.26

(Binford 1984; Grayson 1988). For example, with a MAU value of 520, we would expect 1,040 of each paired element in the skeleton. If only 250 dentaries or maxillae are present, their element survivorship would be 250/1,040, or 24 percent.

As shown in Figure 5 and Table 5, element survivorship is extremely variable; several cranial and paired fin elements show moderate to very high frequencies (basioccipital, opercle, pharyngeal, cleithrum), whereas vertebrae and numerous other elements of the cranium and paired fins are scarce.

To examine the role of bone density in structuring body part representation in prehistoric fau-

Table 6. Comparison of Rank Order Element Density (g/cm^3) with Element Survivorship (Percent MAU).

Element	Density	Rank	% MAU	Rank
Articular			4.1	11
Dentary			7.5	9
First vertebra			18.6	4
Maxilla			1.3	14
Other vertebra			14.3	5
Urohyal			10.4	8
Basipterygium			6.1	10
Pharyngeal			100.0	1
Autopterotic			11.1	7
Scapula			3.7	12.
Coracoid			3.7	12.
Exoccipital			12.7	6
Opercle .			89.1	3
Cleithrum			94.2	2

nal assemblages, Lyman (1984, 1985; Lyman et al. 1992), Kreutzer (1992), and Butler and Chatters (1994) have measured the bone mineral content (g) of modern skeletal elements from artiodactyls, rodents, and salmonids by photon absorptiometry. Combined with estimates of bone volume, their values provide a valid ordinal measure of volume density $(g/cm^3)(sensu$ Lyman 1984), which can be compared with rank-order element survivorships in prehistoric faunas to determine the degree to which bone density structures body part representation.

Although bone density data are not available for tui chub, Butler and Chatters have recently determined element densities for another species in the Cypriniformes order (*Catostomus macrocheilus*, family Catostomidae). I assume that density values for this taxon approximate those for the tui chub. Volume densities of 14 elements were determined; representative cranial, paired fin, and vertebral elements from five *Catostomus* skeletons were studied.

As shown in Table 6, the rank orders of bone density and element survivorship are very different; the correlation is low and not significant (Spearman's rho = -.330, .50 > p > .20). The most striking discrepancy occurs with the opercle and cleithrum, which have close to the highest survivorship and yet the lowest densities. Similarly, the very high abundance of the pharyngeal is not predicted from its only moderately high bone density. The low correlation argues against the role of water action in modifying the assemblage; at least water did not differentially deposit or remove elements of particular density values.

As argued above, a low correlation between density and survivorship is expected if cultural agents in some way modified the faunal materials. The relative scarcity of vertebrae, which have close to the highest densities and yet survivorship of less than 20 percent, may result from differential processing of trunks versus heads. For example, if trunks were consumed and heads were not, or if trunks were cooked with the heads detached, digestion and cooking may lead to greater loss of vertebrae relative to some bones of the head. Given the small chub body size, the low correlation presumably is not explained by differential transport of carcass parts to the site (e.g., Lyman 1985), although the scarcity of vertebrae may indicate that trunks and heads were consumed and deposited in different locations. Because we lack data on the specific effects of cooking and digestion on tui chub bone preservation, other scenarios are equally plausible.

Additional support for the argument that more vertebrae are expected in a natural deposit of cyprinid remains is provided by Stewart's (1991) recent analysis of natural fish bone accumulations from Lake Turkana. Based on analysis of cypriniform body part representation, Stewart suggests that cranial elements survive poorly, whereas vertebral elements survive very well. Although more specific comparisons between Lake Turkana and Stillwater are not possible because of differences in data organization and reporting, Stewart's results certainly indicate that vertebrae are relatively abundant in natural lakeside settings, which is contrary to that found at Stillwater.

Of course identifiability and recovery practices (Lyman and O'Brien 1987) also may affect element representation. Given the small body sizes represented, no doubt the relative infrequency of some elements is explained by the use of 3.2-mm mesh screens during excavation. To examine whether 3.2-mm recovery biased vertebrae representation in particular, I assessed element survivorships for selected elements within a single flotation sample. I included two of the most common cranial elements in the 3.2-mm fraction, the opercle and pharyngeal, and the vertebrae in analysis. These elements provide 436 MNE; ele-

Table 7. Comparison of Survivorship (Percent MAU) between 3.2-mm and 1.6-mm Fraction, Selected Elements, 26CH1062.

Element	1.0	3.2-mm	
	MNE	% MAU	% MAU
Opercle ^a	62	100.0	89.13
Pharyngeal	27	43.5	100.0
First vertebra	14	45.2	18.65
Other vertebra	333	31.2	14.3

^aProvided the largest MAU of 31.

ment survivorship was based on the opercle, which produced a MAU value of 31 (Table 7). Survivorship of vertebrae in the flotation sample is almost double that found in the 3.2-mm mesh, suggesting that a disproportionate number of vertebrae are lost through 3.2-mm mesh (at least relative to opercles and pharyngeals) (Table 7). However, survivorship of most vertebrae in the 1.6-mm mesh is still much lower than 50 percent, suggesting that recovery bias is not a major factor in accounting for vertebrae scarcity.

In sum, tui chub element survivorship is highly variable; some fragile elements of relatively low density (e.g., opercle, pharyngeal) are extremely abundant, whereas many other elements of relatively high density are scarce. Most of this variation is not explained by the intrinsic property of bone density. Although the scarcity of some elements may be explained by archaeological recovery practices, recovery bias does not completely account for the scarcity of vertebrae. Rather, vertebra scarcity is best explained by the actions of agents that differentially treat parts of the fish. Cultural agents seem to be the most likely candidate for this intervention.

Natural vs. Cultural Origin of Stillwater Fish Remains

Archaeologists working throughout the world are beginning to recognize that before we can examine evidence of human fishing strategies, we must be able to distinguish fish bone resulting from natural death and deposition from that deposited by cultural agents. Noe-Nygaard (1983), for example, examined the contribution of natural fish kills in 3,000-year-old lakeside deposits in central Denmark. She posits that the fish remains result from cultural procurement based on the narrow size range of individuals represented and a similar season of capture of the fishes and mammals present. On the other hand, Richter (1986) argues that the extremely small fish remains from a coastal Danish Neolithic site were naturally deposited, based on collagen analysis, showing that the fish remains were not heated. Other investigators have used attributes such as bone discoloration and fragmentation, spatial distribution of faunal materials and their co-occurrence with unambiguous artifacts, as well as hominid dietary preferences to argue whether or not people were primarily responsible for a fish bone accumulation (Butler 1990, 1993; Stewart 1991; Van Neer and Muniz 1993).

Similarly, researchers in the Great Basin of western North America have begun to share this concern for fish bone origin in lacustrine, fluvial, and cave deposits and have started to develop approaches to assess taphonomic agents (e.g., Aikens and Greenspan 1988; Greenspan 1988; Smith 1985). My analysis of primarily tui chub remains from one site in the Stillwater Marsh suggests that humans are primarily, if not entirely, responsible for fish deposition at the site.

A relatively narrow size range of tui chub are represented in the bone bed, which is more suggestive of selective procurement than catastrophic mass death. In particular, the chub body size data suggest that mass harvesting techniques, involving the use of nets of small mesh size, were used to catch the fish. Hamley (1975) and other fisheries researchers (e.g., Gulland and Harding 1961; Jensen 1990; McCombie and Fry 1960) have shown that gill nets of specified mesh size are very selective of fish of particular lengths. Furthermore, a disproportionately low frequency of vertebrae are present, which indicates that some intervening factors, such as cultural processing, may have affected body part representation. Bone surface modification has not helped sort out agents responsible for the fish remains. Importantly, the absence of evidence for human digestion and processing on the bone surfaces has been used to argue for a natural origin of fish remains from other Stillwater sites (e.g., Raven and Schmitt 1991). However, given our limited understanding of how fish bone is modified during digestion and cultural processing, bone surface characteristics are not necessarily useful indicators of depositional origins. The absence of such evidence at 26CH1062, then, does not undermine the argument for cultural origin of the fish bone.

A variety of additional research would greatly increase our understanding of the contribution of natural fish kills in marsh sites. For example, controlled collection and analysis of fish remains deposited after the recent flooding in Stillwater would allow detailed characterization of fish assemblages resulting from natural death and deposition (e.g., Butler 1990, 1993; Stewart 1991). Also, as suggested by Raven and Schmitt (1991), test excavation of marsh deposits free of prehistoric cultural materials would allow us to determine the likelihood of the deposition and preservation of natural fish bone outside archaeological contexts; if such deposits are located, they would help characterize natural fish bone assemblages.

Small Tui Chub—an Important Marsh Resource

As described in the introduction, the debate over the importance of marsh resources to prehistoric economies centers, in part, on the relative value of marsh versus upland resources. Livingston (1991) has recently marshaled archaeological avian faunal data and life history characteristics of waterfowl to argue that birds were an important subsistence component to peoples of the western Great Basin over the past 5,000 years. Drawing on experiments with fish procurement and processing and nutritional analyses, Raymond and Sobel (1990) and Lindstrom (1992) argue that fish would have provided rates of return (calories/hr) as high or higher than terrestrial resources (e.g., Simms 1987), depending on fish body size, methods of processing, and other variables. In particular, Raymond and Sobel (1990) found that small schooling tui chub caught through mass harvesting (nets) had higher return rates than larger chub, because larger fish required more processing time.⁵

Prehistoric evidence for the use of small tui chub is found in several western Great Basin cave assemblages, where Raymond and Sobel (1990) measured the lengths of whole desiccated tui chub from cultural features. Chub in Stick Cave ranged between 75 and 122 mm in total length (mean 99 mm, n = 79), and Lovelock Cave tui chub ranged in total length between 43 and 130 mm (mean 75 mm, n = 51). Body size of the tui chub at Humbolt Cave were larger and more variable, ranging between 90 and 220 mm (mean 148 mm, n = 54). Based on the relatively high return rates of small chub and the archaeological evidence for small chub use, the authors suggest that prehistoric fishers specifically targeted smaller chub in the subsistence quest.

Analysis of fish remains from Stillwater certainly indicates that tui chub, particularly small tui chub, were a major food resource to inhabitants of the Stillwater Marsh. The fish remains in the 26CH1062 assemblage represent over 85 percent of the identified vertebrate faunal remains (Livingston 1991; Schmitt and Sharp 1990). Our sampling of the faunal assemblage suggests that over 290,000 fish remains were recovered during excavation; a small (but unknown) fraction of the site was excavated. Thus, the sampling and analysis of the fish remains suggest that literally hundreds of thousands of small tui chub reside in the archaeological deposit. Such abundance supports the position that small tui chub were a key resource to prehistoric marsh inhabitants.

Many questions remain. How pervasive is this trend across environments and over time? Were small chub targeted by the earliest marsh and lakeside residents of the western Great Basin or has there been an increase in the use of small chub over time? Does the use of small chub represent a decline in foraging efficiency, an example of resource intensification, as Broughton (1994) has documented for the late Holocene of central California based on his study of mammalian and fish faunal assemblages? Did fish resource use vary across aquatic environments in the Great Basin (e.g., deep-water lakes, perennial streams, and marshes), which support different species of fishes with different life histories and growth characteristics? How would this variation constrain human subsistence scheduling and mobility patterns?

Answering these questions will require additional taphonomic analysis of faunal assemblages from other sites in Stillwater and the western Great

Basin. The results discussed here should assist with resolving some of the taphonomic ambiguity surrounding marsh assemblages. In addition, the regression model provided will allow reconstructions of fish body size, which will assist with interpretations of procurement strategies as well as evaluation of resource intensification models (e.g., Broughton 1994) and diet breadth models (e.g., Broughton and Grayson 1993; Madsen 1993). Such models make predictions about foraging efficiency and prey selection, factors at least in part determined by prey body size (e.g., that prey body size is positively correlated with prey rank: the larger the animal, the higher its rank and the greater its return rate). Importantly for tui chub, whether body size per se is an appropriate measure of prev rank may be questionable when mass harvesting techniques are employed in capture. With increased chronological and taphonomic controls over fish assemblages from wetland and cave sites, we will be able to more clearly document the relative importance of fish of various sizes to prehistoric subsistence and how that use may have varied over time.

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Notes

1. This interpretation may explain my failed attempts to identify annuli on the small opercles from the Stillwater archaeological deposit. Many of the chub represented in the archaeological deposit may have expired before the annulus formed, if most of the chub died in their first or second years of life.

2. Opercles are relatively large elements. OL is the largest linear dimension on the element and would constrain the mesh size through which the specimen could pass. The OL from a chub measuring 55 mm SL ranges between 5.2 and 5.8 mm. Opercles would have to be three times smaller than these to pass through 1.6-mm mesh. In short, opercles from fish 15-20 mm SL may be lost through 1.6-mm mesh, but

opercles from fish larger than 20 mm should be represented in the flotation samples if indeed they were deposited and recovered in the sample.

3. Several investigators of mammalian faunas (e.g., Frison 1982; Kurten 1953; MacFadden 1992; Todd 1987) have documented the underrepresentation of neonates and juveniles in fossil assemblages and suggested that such scarcity results from differential preservation. Ontogenetic changes in bone, which would enhance preservation potential of the mature versus young tui chub, certainly need to be considered.

4. Indeed, other research involving modern feeding experiments suggests that bones of some fish are virtually destroyed during vertebrate digestion. A. K. G. Jones (1984, 1986) fed dogs and humans various fishes (cod, herring, and snapper); only between 9 and 17 percent of the fish remains in the feces were identifiable to element. I fed a dog one complete coho salmon (*Oncorhynchus kisutch*) and found only three identifiable remains in the feces: two eye lenses and one vertebra fragment (Butler 1990). On the other hand, the fish remains in the Fish Slough Cave coprolite were relatively well-preserved, representing elements from all parts of the skeleton. Given that the data are archaeológical, the proportion of the carcass originally ingested is not known. The data suggest, however, that bone destruction may not be as great for cyprinids/catostomids as for other fishes examined.

5. Contrary to Raymond and Sobel's (1990) finding that smaller chub had higher rates of return than larger ones, Broughton (1994) uses the Raymond and Sobel data (1990:Table 5) to show that chub length is positively correlated with return rate (Spearman's rho = .671, p = .027) (Broughton 1994:Table 1). Apparently, the discrepancy is due to varying treatments of "costs", particularly "handling time," by the authors. Broughton (1994) uses handling time that includes only the time needed to set and retrieve the net and remove the fish. In addition to this handling time, Raymond and Sobel (1990) also include time needed to process (clean, gut, eviscerate, dry) the fish, which, they note, is much greater for larger fish than for smaller fish.

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