

SUPPLEMENTARY INFORMATION
TAPHONOMY THROUGH FISHEYES:
AN HISTORICAL AND METHODOLOGICAL OVERVIEW

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Supplementary Information Table 1: Selected studies of diagenetic traces on digested fish bones.

Accumulation Agent	Main Taxa	RESULTS		References
		General results	Diagnostic features	
Human	Atlantic herring (<i>Clupea harengus</i>)	Less than 10% of ingested fish bones passed through the digestive system.	Crushed vertebrae. Some vertebrae without modifications.	(Jones 1986)
Pig (<i>Sus domesticus</i>)	Atlantic herring (<i>Clupea harengus</i>) Mackerel (<i>Scomber scombrus</i>)			
Dog (<i>Canis familiaris</i>)	Atlantic herring (<i>Clupea harengus</i>) Haddock (<i>Melanogrammus aeglefinus</i>)		Haddock otoliths with signs of digestion (polished surface). The process of digestion reduced the size of the otoliths by <i>ca.</i> 2mm.	
European otter (<i>Lutra lutra</i>)	European eel (<i>Anguilla anguilla</i>) <i>Salmo</i> sp. Cyprinidae Gadidae Labridae Pleuronectiformes etc.	Remains of fish below 150 mm Total Length. Minimal damage to fish bones, with a representation of almost all the anatomical elements. Bones from larger fish more etched.	Crushing, chewing, and etching. Small fish remains intact, larger fish exhibit signs of chewing. Cleithrum and opercular are the most frequently fragmented bones.	(Nicholson 1991)
Grey seal (<i>Halichoerus grypus</i>)	Gadidae Ammodytidae Pleuronectiformes Elasmobranchs	Limited number of bones retrieved. Mostly small vertebrae present. Variable damage. Damage mostly involved crushing and erosion, with larger otoliths and vertebrae displaying more substantial damage.	Larger vertebrae exhibit signs of chewing, and the centrum gets thinner. Small vertebrae show evidence of crushing and/or reduced surface erosion. Otoliths from small fish intact, those from large fish broken and eroded. Teeth exhibit “pitting”.	
Sea gull (<i>Larus argentatus</i> ; <i>Larus marinus</i>)	Gadidae	Scarce number of fish remains. Body lengths (Total length) ranging from 150-500 mm.	Various types and degrees of damage, including bone fractures and acid erosion. No signs of chewing. Otoliths exhibit no signs of erosion. Large vertebrae lost neural and haemal processes, with some appearing to be tumbled. Identification from other agents proved challenging.	(Nicholson 1991)

Human (<i>Homo sapiens</i>)	Juvenile Atlantic herring (<i>Clupea harengus</i>) Sprat (<i>Sprattus sprattus</i>) European pilchard (<i>Sardina pilchardus</i>)	Only a small proportion of bones survived; almost all cranial bones destroyed. Most of the recovered bones sustained damage.	Most vertebrae crushed, some featuring black or brown stains, and others etching. Extreme acid dissolution is evident, marked by crenellation and rounding of edges and/or articular facets. Unidentifiable fragments with smooth crenellated edges. Some vertebrae without any signs of alteration.	(Nicholson 1991, 1993)
Human (<i>Homo sapiens</i>)	2500 identified remains (56% otoliths), representing 70 marine species including: Clupeidae Sparidae <i>Engraulis encrasicolus</i> <i>Sardina pilchardus</i> Scombridae <i>Spicara</i> sp.	300 otoliths recovered. Small seabreams (Sparidae) represent 63% of the recovered fish (MNI=84). Large number of anchovies & mackerel and lower numbers of sea bass, eels, garfish, wrasse, picarels, damsel fish, and mullets. Remains representing complete fish may indicate a fish sauce.	Primarily small marine species from coastal waters. Numerous otoliths and most skeletal elements recovered. Chewed and corroded bones. Mineralized scales provide evidence of cooking prior to consumption. Probably consumed as sauce (i.e., condiment). Cranial elements are missing. Very small bones too fragmentated to allow recording.	(Nicholson et al. 2018; Rowan 2014)
Human (<i>Homo sapiens</i>)	Tui chub (<i>Gila bicolor</i>)	Articular, basioccipital, ceratohyal, pharyngeals, opercle, and caudal vertebrae selected for analyses. Surface morphology modifications examined using SEM. Bone loss limited (might be attributed to variation in bone structure and density among species). Digestive processes often modify specimens yet a significant fraction of remains also unaffected. Digestive processes of humans and coyotes generate similar modifications to fish remains. Challenging to differentiate remains generated by coyote and human digestive processes.	Pitting: scarce. Rounding: scarce. Deformation: most vertebrae highly deformed. Staining: dark color. Fragmentation: present. The occurrence of these attributes exhibits a high degree of variability; attributes not deterministically linked to digestive processes (i.e., equifinality).	(Butler and Schroeder 1998)
Coyote (<i>Canis latrans</i>)			Pitting: numerous elements. Rounding and deformation: < 50% Color: whitish. Adhering organic tissue. Fragmentation.	
African fish eagle (<i>Haliaeetus vocifer</i>)	1551 identified remains representing 11 taxa including: Cyprinidae Clariidae Schilbeidae Mochokidae Distichonidae Cichlidae Latidae	Collected from roosting sites at Lake Turkana, Kenya. Dominant taxa: Cichlids and catfishes (Clariidae and <i>Synodontis</i>); also <i>Hydrocynus forskali</i> .	Abundance of juveniles (small bones). The taxonomic composition of the fish remains was compared with data from the local fish community. Prey selectivity index calculated.	(Stewart et al. 1997)

Barn owl (<i>Tyto alba</i>)	Tui chub (<i>Siphateles bicolor</i>)	High proportion of element survivorship. Collected fish correspond to specimens ranging between 10-75 g.	Minimal fragmentation: 92% of the elements at least 66% complete. Deformation on the vertebrae. Scarce evidence of digestion damage.	(Broughton et al. 2006; Cannon et al. 2006)
Eurasian Eagle Owl (<i>Bubo bubo</i>)	Brown trout (<i>Salmo trutta</i>) Pike (<i>Esox lucius</i>) European carp (<i>Cyprinus carpio</i>) Common chub (<i>Leuciscus cephalus</i>) Common barbel (<i>Barbus barbus</i>) Iberian nase (<i>Chondrostoma toxostoma</i>) European perch (<i>Perca fluviatilis</i>)	Fish represent a small proportion on the diet of this prey bird. Spatial patterning: regurgitated remains accumulate on spatially defined “deposits”.	No information.	(Russ 2010)
European otter (<i>Lutra lutra</i>)	Brown trout (<i>Salmo trutta</i>) Common rudd (<i>Scardinius erythrophthalmus</i>) Eurasian minnow (<i>Phoxinus phoxinus</i>) Common chub (<i>Squalius cephalus</i>) Common dace (<i>Leuciscus leuciscus</i>) European perch (<i>Perca fluviatilis</i>) Pumpkinseed (<i>Lepomis gibbosus</i>) European bullhead (<i>Cottus gobio</i>)	Fish comprised 82% of remains identified in spraints. 90% of these exhibited characteristic signs of biochemical modifications, particularly rounding and polishing. Non-digested fish bones accounted for 9.8% of the faunal material. Otters consumed animals ranging between 10-200g. Remains of Cyprinids, Percids and Centrarchids displayed moderate digestion, whereas Salmonids featured extreme digestion marks on a far higher proportion. Simultaneous presence in the same spraint of complete and fragmentary bones.	Vertebrae exhibit deformation, either compression or twisting. Tooth marks and puncture marks evident on vertebrae. Some bones show signs of chewing and/or crushing. The surface of some bones characterized by a smooth and polished texture, rated as moderate (56%) or intensive digestion (see Fernández-Jalvo and Andrews 2016).	(Guillaud et al. 2017; Guillaud et al. 2014)
Eurasian Eagle Owl (<i>Bubo bubo</i>)	Allis shad (<i>Alosa alosa</i>) European eel (<i>Anguilla anguilla</i>) Gudgeon (<i>Gobio gobio</i>) Common roach (<i>Rutilus rutilus</i>) Mediterranean barbel (<i>Barbus meridionalis</i>) Common chub (<i>Squalius cephalus</i>) Tench (<i>Tinca tinca</i>)	All skeletal elements are present in samples. Relatively complete skeletal representation with minimal bone fragmentation and slight digestive surface damage. Simultaneous presence of complete and fragmented elements in the same pellet. Intensity of digestion variable. Fracturing of skeletal elements infrequent. More than 86 % of bones do not exhibit any modification.	Deformation of skeletal elements rare. Fissures (NISP = 7), exfoliation (NISP = 9), and perforation (NISP = 7) observed on the surface of specific cranial bones and vertebrae, along with twisted bones (NISP = 2). Damage to bone surfaces is attributed to beaks. SEM (scanning electron microscopy) revealed rounding and polishing of articular surfaces in vertebrae. Advanced degradation and digestion holes (Fig. 3) on 2 % of the sample.	(Guillaud et al. 2018)

Yellow-legged Gull (<i>Larus michahellis</i>)	European pilchard (<i>Sardina pilchardus</i>) Round sardinella (<i>Sardinella aurita</i>) European anchovy (<i>Engraulis encrasicolus</i>) European eel (<i>Anguilla anguilla</i>) European hake (<i>Merluccius merluccius</i>) Atlantic horse mackerel (<i>Trachurus trachurus</i>) Bogue (<i>Boops boops</i>) White seabream (<i>Diplodus sargus</i>) Stripped seabream (<i>Lithognathus mormyrus</i>) Axillary seabream (<i>Pagellus acarne</i>) Common pandora (<i>Pagellus erythrinus</i>) Red porgy (<i>Pagrus pagrus</i>) Salema (<i>Sarpa salpa</i>) Grouper <i>Epinephelus</i> sp.	56 regurgitation pellets. Only 3% of the elements lack traces of digestion. Eel, sea breams, and grouper exhibit no traces of digestion. Carangidae remains exhibited moderate digestion for most parts. Clupeidae, Engraulidae, and Merlucciidae bones were all heavily altered by digestion. Within a single pellet, the intensity of digestion can vary from bone to bone, as this may depend on the type of bone and on how long ingestion lasted. Estimated body mass ranged from <10 to 200 gr (10–30 cm total length) and up to 2000 gr (40 cm total length) for the white sea bream.	Signs of abrasion and fragmentation. Infrequent signs of deformation on skeletal elements. Rounding and polishing of articular margins evident with SEM. SEM shows advanced degradation and digestion pits. Among visible alterations abrasion or polishing marks dominant (NISP = 1141); fissures (NISP = 37), and exfoliation (NISP = 34) much scarcer. Otoliths and eye lenses are well preserved without any evidence of alterations.	(Guillaud et al. 2019)
European otter (<i>Lutra lutra</i>)	Salmo trutta, (Salmo) Perch (<i>Perca fluviatilis</i>), Pumpkinseed (<i>Lepomis gibbosus</i>), Rudd (<i>Scardinius erythrophthalmus</i>), common minnow (<i>Phoxinus phoxinus</i>), European bullhead (<i>Cottus gobio</i>)	Low frequency of compression signatures in vertebrae. Presence of twisting and tooth marks on vertebral centra. Clear features of digestions in vertebrae.	Deformation of vertebrae caused by masticatory action. Digestive traces include rounding and polishing of the spikes, crests and trabeculae, along with a smoothing and thinning of the trabeculae and a concomitant widening of the vertebral lacunae . Presence of random cracks.	(Frontini et al. 2019; Frontini et al. 2021)

Supplementary Information Table 2: Selected studies on fish procurement practices and their effects on fish remains.

Taxon	Location	Evaluated process + details	Main results	References
Rockfish (<i>Sebastes</i> sp.)	Richardson Island site, Haida Gwaii, British Columbia, Canada.	Burning as an agent of shrinkage on fresh bones. Elements measured: atlas, axis, vomer, dentary, premaxilla, epihyal, maxilla, basioccipital, and otoliths. Bones burnt at 900°C.	Burning caused substantial size reduction of bones, with an average shrinkage of 9%. Otoliths do not survive high temperatures (900°C). Extensively fragmented bones become unrecognizable, deflating NISP.	(Steffen and Mackie 2005)
Herring (<i>Clupea harengus</i>) Cod (<i>Gadus morhua</i>) Whiting (<i>Merlangius merlangus</i>) Plaice (<i>Pleuronectes platessa</i>)	Bradford, England.	The impact of thermal alteration on the survival of fish remains. Fish cooked with different methods, in different types of fire. Isolated bones also burnt. Parameters included: color, macroscopic and microscopic structure, using SEM. Bone strength examined by a static bending test performed with an Instron table testing instrument.	Survival depends on the location of remains within the fire, heat temperature, length of exposure to maximum heat, and time in the fire. Although most remains did not survive burning, some did, regardless of body size. Bone color differed according to the type of bone, its size, and the duration of exposure at maximum temperature.	(Nicholson 1995)
European carp (<i>Cyprinus carpio</i>) Common bream (<i>Abramis brama</i>) Common rudd (<i>Scardinius erythrophthalmus</i>) Common bleak (<i>Alburnus alburnus</i>) Crucian carp (<i>Carassius carassius</i>) Tench (<i>Tinca tinca</i>) Common chub (<i>Leuciscus cephalus</i>) <i>Barbus</i> sp. <i>Chondrostoma</i> sp. <i>Rhodeus</i> sp. Siluridae	Dispilio site, SW Lake Orestis, Kastoria, NW Greece.	Ca. 20,000 water-logged fish remains examined to determine the cause of bone alterations, including evidence of cooking and burning. Recorded features: Color alterations, structural modifications of the surface, and surface texture (cracks and deformations). Techniques: SEM, EDXA (X- ray Microanalysis), FTIR, and histological sections.	Comparative assessment of spatial distribution of remains with regard to site installations and the ancient lake shore. Evidence of different butchering methods on large carps and catfish (e.g., removal of caudal portions). Examination of the processes involved in the development of “Black colored bones”: heat treatment vs. oxide staining. Examination of the splitting factor to reveal CS changes caused by heat . Dark coloration may have been caused by mineral staining and/or burning. Histological sections exhibited micro-cracks that were not characteristic of either burning or cooking.	(Stathopoulou et al. 2013)

Tiger fish (<i>Hydrocynus</i> sp.) Nile perch (<i>Lates niloticus</i>) <i>Alestes</i> sp. <i>Barbus</i> sp. <i>Bagrus</i> sp. <i>Clarias</i> sp. <i>Synodontis</i> sp. Cichlidae	Lake Turkana, Kenya.	Recognizing culturally altered fishbone assemblages.	Fishermen had selective taxonomic and size preferences: targeting mainly medium-sized Cichlids and <i>Clarias</i> sp. Differential butchering methods body size dependent: Small fish processed whole while those above ~50 cm (TL) had their heads detached from the body. Traces of burning recorded on 20% of the cranial bones from large fish. Cut marks appeared on 4% of the bones from both small and large fish. Most cut marks were located on the laterals of the skull	(Stewart 1989, 1994; Stewart and Gifford-Gonzalez 1994)
Freshwater and marine species.	Sindh coast, Pakistan.	Recognizing fish butchery methods.	Butchery dependent on fish processing method, size, and group, with a difference existing between bony and cartilaginous fish. In sharks and rays, most skeletal elements and entrails were discarded. In bony fish, gills, entrails, fins and tails were discarded. People of a lower economic level tend to buy inexpensive parts of the fish (heads and tails). Cut marks are rare, appearing mainly on ribs, vertebrae, and cranial bones.	(Belcher 1994, 1998, 2011)
Pacific crevalle jack (<i>Caranx caninus</i>) Shining grunt (<i>Haemulopsis nitidus</i>) Sculpured sea catfish (<i>Notarius kessleri</i>) Box sea catfish (<i>Cathorops multiradiatus</i>) Chili Sea catfish (<i>Notarius troschelii</i>)	Parita Bay, Panama.	Fish preparation areas, butchering methods used for immediate consumption and long-term preservation, according to species and body size. Extent of fragmentation evaluated using a weighted mean index of fragmentation (WMI). Bone survival calculated from a survival index (SI), calculated from the observed abundance of bones, compared with that expected in a complete animal.	Three butchering methods documented: two applied on bony fish and one on sharks. Butchering method depends on the species, size, amount of fat, and freshness of each specimen. Method 1: fish processed complete with the skull intact. Incision performed along the ventral midline. Method 2 (“Butterfly fish”): a dorsal incision splits the fish, including the skull, in two halves which remain together. Method 3: Filleted straps of shark meat. All skeletal remains discarded. Entrails discarded onboard or fed to domestic animals. Butchering method recognized on archaeological specimens from skeletal spectra, fragmentation patterns, and state of preservation of the bone.	(Zohar and Cooke 1997; Zohar and Cooke 2019)
Rivulated rabbitfish (<i>Siganus rivulatus</i>) Brown surgeonfish (<i>Acanthurus nigrofasciatus</i>) <i>Scarus</i> sp.	Nabek, Southern Sinai, Egypt.	Fish preparation areas, butchering methods applied for immediate consumption and long-term preservation, according to species and body size.	Entrails discarded in the sea. Fish butchered according to the “Butterfly cut” method (see above) regardless of body size or species. Fish dried in the sun.	(Zohar and Cooke 2019)

Spotted weakfish <i>(Cynoscion nebulosus)</i> Red drum <i>(Sciaenops ocellatus)</i> Hardhead catfish <i>(Ariopsis felis)</i> Summer flounder <i>(Paralichthys dentatus)</i>	Oregon.	Understanding cutmark traces on fish remains following butchering and burial.	27 months after burial, 76% of the originally visible cutmarks disappeared. Most cut marks appeared on the vertebral centra. No correlation found between soil pH and bone preservation.	(Willis and Boehm 2014; Willis et al. 2008)
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Supplementary Information Table 3: Selected experimental studies on processes affecting fish bone survival.

Taxon	Skeletal element	Evaluated process	Main results	References
Dogfish (<i>Scyliorhinus canicula</i>) Herring (<i>Clupea harengus</i>) Cod (<i>Gadus morhua</i>) Haddock (<i>Melanogrammus aeglefinus</i>), Plaice (<i>Pleuronectes platessa</i>)	Complete skeletons, except for dogfish (only vertebrae)	Sedimentary abrasion on fresh and cooked fish in comparison to mammals, amphibians and birds.	Bone loss is related to shape and original condition. Robust fish bones (neurocranium) and spherical bones (vertebrae) survive best. Regarding the original state, boiled bones were destroyed faster than fresh bones. Among the different boiled taxa, fish bones were destroyed faster than those of mammals.	(Nicholson 1992)
Cod, (<i>Gadus morhua</i>) Whiting (<i>Merlangius merlangus</i>) Plaice (<i>Pleuronectes platessa</i>) Herring (<i>Clupea harengus</i>)	Complete skeleton	Diagenesis of cooked and uncooked fish bone after burial in different soil types and comparison to mammals and birds. Long-term experiment (7 years).	Boiled bones are more degraded than uncooked bones in the different soils. No bone degradation pattern could be established. Key variables of bone degradation include local environmental conditions and microorganisms.	(Nicholson 1995)
Meagre (<i>Argyrosomus regius</i>),	Premaxilla, Hypohyal, Ceratohyal, Epihyal, Opercle Caudal vertebrae	Experiments on: Abrasion due to dry sand. Abrasion in sand with water.	Dry sand abrasion preserves fish bones' fibrous tissues. Rounding of salient angles, pitting, and scratches often recorded. Sand and water abrasion obliterates fibrous tissues. Scratches and pitting never recorded.	(Frontini et al. 2019)
	Ceratohyal	Impact of sand grains on bone surfaces.	On dry fish bone abundant pitting on bone surface and dispersed scratches were recorder. When fish bone is fresh, the pitting on bone surface is few and there are dispersed scratches.	
	Ceratohyal	Trampling	Compression of dry fish bone on a dry sandy substrates forms pitting associated to scratches. Compression of hydrated fish bone on a dry sandy substrate forms pitting with deformed edges associated to scratches.	
Meagre (<i>Argyrosomus regius</i>), European hake (<i>Merluccius merluccius</i>) Pouting (<i>Trisopterus luscus</i>)	Vertebrae	Experimental uniaxial compression. Evaluation of the role of vertebral size on fragmentation due to compression	Vertebrae subjected to uniaxial compression feature diagnostic mechanical modifications in the physical structure of the bone which can be identified on archaeological specimens. Compressive forces applied to dry vertebrae generate brittle deformation and fragmentation., In hydrated vertebrae, compressive forces generate plastic deformation without mechanical failure.	(Frontini et al. 2023; Frontini et al. 2021; Morales-Muñiz et al. 2021)

<i>Oncorhynchus mykiss</i> <i>Salmo salar</i> <i>Salmo trutta</i>			Criteria for identifying bone condition prior to compression: Dry specimens: a) A fracture that runs along the midpoint of the vertebral centrum; b) Bone tissue detaching from the centrum. Wet specimens: a) Mild elliptical contour of the centrum; b) Indentations on the outer edge of the centrum; d) A pleat that runs across the vertebral centrum, from the center to the edges. The key feature that determines the effects of compression on fish vertebrae is the original condition of the bone (i.e., dry, fresh, hydrated), rather than the size of the vertebra. Three types of lateral fragmentation can be identified after compression: mild, extensive and total.	(Frontini et al. 2023; Frontini et al. 2021; Morales-Muñiz et al. 2021)
Barracuta (<i>Thyrsites atun</i>)	Non-diagnostic bone (i.e. bone excluding the five paired cranial bones: dentary, quadrate, articular, premaxilla and maxilla).	Physical appearance of bone. Color. Degree of alteration. Percent of nitrogen (a proxy of total collagen content).	Discoloration manifested as an orange hue on the bones. FTIR (Infrared Spectroscopy) used to assess collagen stability . Nitrogen concentration for protein as proxy of state of preservation (>40% extractable collagen). Five categories to describe a bone's state of preservation. Well preserved bones can be used for radiocarbon dating.	(Petchey and Higham 2000)
Lake Whitefish (<i>Coregonus clupeaformis</i>)	Cranial bones and vertebrae.	Effect of soil pH (4 & 10), cooking methods (i.e., boiling and burning) and different temperatures on the survival of salmon bones.	Burnt cranial bones destroyed more quickly and featuring a greater weight loss when compared with vertebrae. Burnt vertebrae and boiled cranial bones lose weight at the same rate. Element destruction increases with heating. Weight loss is similar under alkaline and acidic conditions.	(Lubinski 1996)
Atlantic Cod (<i>Gadus morhua</i>) Atlantic Herring (<i>Clupea harengus</i>) Rainbow Trout (<i>Oncorhynchus mykiss</i>) Japanese Amberjack (<i>Seriola quinqueradiata</i>) Nile tilapia (<i>Oreochromis niloticus</i>)	Fish bone powder.	Alteration of chemical properties (collagen Type I) due to different temperatures, in cold-water and warm-water fish.	Archaeological fish species composition is affected by the thermal stability of collagen (Type I). The decrease of collagen type I stability originates a reduction in the complete bone stability.	(Harvey et al. 2021)

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