9. FISH

W. P. PATTERSON (wppatter@syr.edu)
Department of Earth Sciences
204 Heroy Geology Laboratory
Syracuse University
Syracuse, NY 13244, USA

G. R. SMITH (grsmith@umich.edu)
Museum of Paleontology
University of Michigan
Ann Arbor, MI 48109, USA

Introduction

Freshwater fish remains are abundant in some water-laid sediments in every time period since the Ordovician. Fish fossils and associated data are useful to estimate conditions in paleoenvironments because living fish respond directly to chemical and physical parameters as well as geological processes (Schaffer, 1972; Behrensmeyer & Kidwell, 1985; Wilson, 1988a, 1988b; Weigelt, 1989; Martin, 1999). Known habitat restrictions of fish and other organisms yield environmental evidence in the fossil record. This evidence is seen first as presence or absence of indicator organisms, but also as in the form of clues about the death and transport of the organisms (taphonomy). Taphonomic information comprises observations not only from transport and decay of carcasses, but also from coprolites that indicate food habits and microorganisms (Bradley, 1946), evidence caused by feeding processes (Gregory et al., 1974; Cate & Evans, 1994; Wilson, 1987), and biogeochemistry of clasts and concretions (Martill, 1988; 1991). These lines of evidence are subject to evaluation by standard experimental, sedimentary, and geochemical methods (Tan & Hudson, 1974).

Many fish live in and are often restricted to habitats that are distinctive depositional environments, as observed by fishermen everywhere. As fossils, species and higher taxonomic groups may provide ecological and environmental evidence about ancient bodies of water (Grande, 1980). Inference from the presence or absence of species or other taxonimic groups is less direct than taphonomic evidence, because environmental interpretation requires the assumption that the fossil organisms had habitat requirements analogous to those of their recent counterparts (Elder & Smith, 1984, Elder & Smith, 1988; Wilson, 1988b). The contribution of fish paleoecological analogy to paleolimnology is limited to

situations in which members of evolved groups of fishes share constrained relationships to such things as current or wave energy, gradient, elevation, temperature, oxygen, salinity, alkalinity, and other chemical conditions in lakes and streams. The basic premise is that ecological and evolutionary responses of fishes–their adaptive shapes, physiology, and especially restriction to aspects of water chemistry, energy, and temperature–are products of long-term interactions between geological processes and natural selection, paralleling the well-known responses of micro-organisms like foraminifera or plants like redwoods to their environments (e.g., Wolfe, 1971). When environments are too ancient to permit evolutionary/ecological analogies based on the relatedness of groups of organisms (Trewin, 1986), or generalities based on observable features such as body shape, evidence is limited to sedimentology, taphonomy, and geochemistry.

Fractionation of isotopes in geochemical systems is proving to be a powerful toolkit for reconstructing temperature, seasonality, salinity, and pathways of incorporation of inorganic and organic carbon sources in foodwebs (e.g., Swart et al., 1993; Patterson et al., 1993; Drummond et al., 1993). Isotope geochemistry of fish otoliths and bones promises to become a new field in itself, but the classical tools-stratigraphy, taphonomy, and taxon adaptations-still provide basic information not available by other means. Herein we present the types of information that may be derived through the analysis of fish remains recovered from sediment in eight categories.

Establishing the stratigraphic framework

Reconstructing the timing of sedimentary events is fundamental to understanding paleoen-vironments (Wilson & Barton, 1996; Smith et al., in press). Evolutionary and ecological processes are often helpful. Fishes and mollusks, for example (Taylor & Smith, 1981), evolve through time slowly and species are restricted to limited times and sedimentary basins. Their evolved responses are recognizable in the fossil record over tens of thousands to millions of years.

Short-term ecological responses, such as rapid growth rates or polymorphic tooth forms, may be observed on a geologically instantaneous time scale. Evolved changes enable stratigraphic diagnosis of sedimentary units whose boundaries may be indistinct because lacustrine depositional units are often formed by reworking earlier formations. Fishes and other fossils provide an index of time to which the physical and chemical changes can be linked (Wilson, 1977, 1996; Grande, 1980; Bell et al., 1989; Smith 1987). These may be calibrated through their known time range in nearby sequences. The evidence thus obtained assists interpretation of the time scale of observed ecological succession as well as the geographic extent of aquatic systems.

Fish are often integral, interacting parts of depositional systems. When lakes are oxygenated to the bottom, benthic inhabitants disturb the bottom while feeding or hiding from predators. Benthic feeders stir up sediments while locating and consuming benthic crustaceans, mollusks, and fishes. Bioturbated sediments may show evidence of fish burrows, nests, concavities, and traces that differ according to the species and sizes of the fishes in the fauna and indicate limnological conditions required for these behaviors and these taxa (Johnson et al., 1984). Observations from submersibles in Lake Superior showed that benthic sculpins disturb soft sediments to a depth of 3-4 centimeters when hiding, or 7-10 cm when nesting (Smith, unpublished data). Predatory freshwater cods create meter-scale

trenches as traps for prey fishes. These allow reconstruction of history from upper sediment layers when bottom conditions permit employment of a sediment camera from a submersible or ROV (Boyer et al., 1989, 1990). Such evidence from behavioral ecology has the potential to constrain estimates of depth, temperature, and oxygen concentration. Interpretation of these traces in the ancient sedimentological record requires outcrop exposures that can be brushed out or recorded by acetate peels. Because the scale of sedimentological features ranges from tens of centimeters to meters, the evidence would not be recognizable in cores. The identity of the organisms causing the trace fossils requires associated presence of identifiable bony remains.

Geomorphology and paleohydrology

Knowing when and where lakes overflowed, drained, and had connections to neighboring lakes (paleohydrology) is important to paleolimnology because it permits reconstruction of the limits and sources of ancient lakes. Aquatic organisms such as fishes, mollusks, and crayfish may be faithful indicators of past aquatic connections, for example, because their presence in sediments of now-separate basins indicates continuous habitat in ancient times, as noted by early naturalists (Cope, 1883; Jordan, 1905). Fish, mollusk, and crayfish species are restricted to water habitat, therefore comparison of species distribution patterns in ancient sediments and recent basins can indicate stream captures, separation of watersheds by tectonic and volcanic barriers, connections among lakes (Hubbs & Miller, 1946), and former lake outlets (Wheeler & Cook, 1954). Occasionally, fish-derived evidence for past drainage connections is reinterpreted as transfer of aquatic organisms on birds' feet (Brown & Rosen, 1995; Spencer & Patchett, 1997). However, ecological tests of alternative hypotheses (Taylor, 1960, 1985; Smith et al., 1982) in western North America always support interpretations based on population ecology, rather than interpretations that rely on dubious rare occurrences, especially where integrated faunas are involved (Taylor, 1985), or where geomorphic data corroborate the biogeographic hypotheses (Smith et al., in press). Chance transport of fish eggs on birds' feet or adult fish in water spouts might be invoked to explain isolated occurrences that are inexplicably "out of place," but whole, ecologically congruent faunas require biogeographic connections through ecological and geochemically compatible habitats. Analysis of communities is important, because different species have non-congruent adaptations for dispersal.

Geochemical investigations add strength to hypotheses regarding fish migrations (Kennedy et al., 2000; Joukhadar et al., 2000). Analysis of trace elements, calcium and strontium ratios, and stable isotopes in accretionary skeletal structures, can indicate whether paleoenvironments had connections to the sea (Koch et al., 1992; Shuck et al., in prep.) by documenting marine isotopic composition in migrants that have fed and grown in the sea (Patterson, 1999). Bones and otoliths in particular offer the most promising chemical record of paleoenvironmental information that may be recovered from fish.

Otoliths

Otoliths are accretionary aragonite structures precipitated within the ears of most teleost fish making them readily analyzed structures, when available. Otoliths are common teleost

fossils that are found in a wide variety of sedimentary environments as old as the Devonian Period (e.g., Nolf, 1995). Well-preserved aragonitic otoliths can be recovered from sedimentary rock dating back at least to the Jurassic (Patterson, 1999), unconsolidated sediment (e.g., Smith & Patterson, 1994), and archaeological deposits known as middens (e.g., Patterson, 1998; Wurster & Patterson, 2000). Otoliths are most commonly recovered by sieving unconsolidated or loosely consolidated sediment. Similarly, otoliths can be recovered from clay and shale that has been broken up by sonication and then sieved. Nolf (1995) provides an excellent summary on the secular distribution of fossil otoliths and their use as taxonomic paleoenvironmental indicators.

Taxonomic identification to the species level is relatively straightforward because otoliths are morphologically distinct (e.g., Nolf, 1995). Modern fish are often restricted to characteristic environmental conditions and life histories, so that related fossil assemblages can be used to reconstruct paleoenvironmental conditions (including bathymetry, ecology, and climate). Otoliths can often be found throughout sequences of rock and sediment, where they offer the potential of providing long-term secular environmental trends, but they are perhaps most valuable as snapshots of paleo-limnology and paleo-weather as revealed by microchemistry.

Thin sections of otoliths reveal annual (and sometimes daily) accretionary growth rings that represent different life stages that may be microsampled for isotopic analysis. Microsampling isolates time-specific aragonite from these growth rings that record temperature and other life history information as changing $\delta^{18}O_{(CaCO_3)}$ and $\delta^{13}C_{(CaCO_3)}$ values (Patterson et al., 1993; Smith & Patterson, 1994; Patterson, 1998; Wurster & Patterson, 2000). Fish that occupy a single environment throughout life will record seasonal conditions for that environment (e.g., seasonal temperature variation in shallow water). Migratory fish will record environmental conditions along the migratory route (e.g., freshwater to marine, or shallow to deep-water transitions). Transitions to marine water and/or cold water will each result in an ontogenetic (life history) increase in isotope values (Patterson, 1999, 2000; Patterson et al., 2000). The laminar bone of fish vertebrae and scales is accretionary, displaying clearly visible annual growth rings. However, isotope analysis of apatite requires time-consuming wet chemistry and offline extraction techniques to quantitatively separate oxygen from the phosphate radical for isotope analysis (O'Neil et al., 1994). Other bones may be resorbed and re-grown during the life of the animal, erasing previously stored isotope information. Otherwise, temperature and $\delta^{18}O_{(H_2O)}$ values are stored as $\delta^{18}O_{(PO_4)}$ values in a manner similar to that of carbonate ($\delta^{18}O_{(CaCO_3)}$). For example, deepwater sculpin (*Myoxocephalus thompsoni*) live at approximately 4°C throughout their adult life, thus precipitating bone apatite and otolith carbonate as $\delta^{18}O_{(PO_4)}$ and $\delta^{18}O_{(CaCO_3)}$ values, respectively. Because the temperature of the water is 4°C and the isotope value of the bone and carbonate can be determined, the $\delta^{18}O_{(H_2O)}$ value can be calculated using empirical temperature fractionation relationships (e.g., Patterson et al., 1993; Smith & Patterson, 1994).

Evaporation/precipitation

$\delta^{18}O$ values of lake-water can serve as an important indicator of precipitation, evaporation, recharge and residence time. Determination of $\delta^{18}O$ values of paleo-water is generally difficult because fractionation relationships require data for both temperature and water

$\delta^{18}O$ values (Fricke & Rogers, 1997). $\delta^{18}O_{(H_2O)}$ values of paleo-lakes can be calculated if the thermal life history of a fish can be constrained. For example, stenothermic species (such as the deepwater sculpin) are restricted to a narrow range of temperatures by the thermal activity range of their enzymes. If this preferred temperature is quantified, $\delta^{18}O$ values of fossil carbonate (fish otoliths) or phosphate (fish bone) can be used to quantify $\delta^{18}O_{(H_2O)}$ values. Fossil fish and modern relatives that belong to the same taxonomic group often have similar thermal tolerances.

Deep, temperate, dimictic lakes that contain deepwater fish are easier to analyze because carbonate from otoliths or bones of benthic fishes in such lakes with a hypolimnion at 4°C enable solving the equation with oxygen isotope values from tissues grown at 4°C. For example, $\delta^{18}O_{(PO_4)}$ and $\delta^{18}O_{(PO_4-CO_3)}$ values of fossil deepwater sculpin, *Myoxocephalus idahoensis*, permit calculation of paleo-water $\delta^{18}O_{(H_2O)}$ values in Pliocene Lake Idaho (Idaho, USA), because *Myoxocephalus* is restricted to hypolimnic 4°C water (Smith & Patterson, 1994). $\delta^{18}O_{(H_2O)}$ values of seasonally cool lakes can also be determined using eurythermic fishes with a characteristic minimum growth temperature by assuming that the highest $\delta^{18}O_{(CaCO_3)}$ value each season equates with the minimum growth temperature (Patterson et al., 1993; Patterson, 1998; Wurster & Patterson, 2000). Because temperature (minimum growth temperature in this instance) and $\delta^{18}O_{(CaCO_3)}$ value are known, $\delta^{18}O_{(H_2O)}$ values can be calculated.

Seasonal variability from micromilled otoliths

The accretionary nature of otoliths coupled with recent advances in micromilling technology (Patterson et al., 1993; Wurster et al., 1999) enable extraction of high-resolution aliquots of aragonite that represent a time averaging of a few weeks to as little as several hours. These samples provide a proxy for details of paleoclimate (Smith & Patterson, 1994; Patterson, 1998; Wurster & Patterson, 2000) and life history (Joukhadar et al., 2000; Patterson et al., 2000) at a resolution that was previously unobtainable. Micromilled otoliths yield $\delta^{18}O$ and $\delta^{13}C$ values that reflect temperature and metabolism for restricted times and habitats.

A polished otolith thin section attached to a stage beneath a fixed micro-milling head, is viewed on a large-screen monitor through a color digital camera (Fig. 1). Growth bands (analogous to tree rings) generally resulting from variable accretion rates in biogenic carbonates are digitized in real-time as a series of three-dimensional coordinates (Fig. 2a). Intermediate coordinates are interpolated using a cubic spline fit through the digital points (Fig. 2b). Intermediate sampling paths, which mimic less visible daily growth banding, are in turn calculated between digitized curves. Sampling path arrays guide three high precision actuators, which position the sample stage relative to the fixed micro-milling head. A fourth actuator provides vertical control of the digital color camera (compensating for vertical movement of the z-axis stage actuator) keeping the specimen image focused.

The micromill uses a diamond dental drill bit to mill discrete carbonate sample aliquots from the otolith. Since the dental drill bit is significantly larger than the requisite width of the sample path, removal of discrete samples requires that the sample paths (for example 15 μm) are milled perpendicular to growth axes using the edge of the drill (Fig. 2c). The width of the carbonate milled depends on the total number of intermediate paths calculated. The volume of sampled carbonate depends on the length, width, and depth of the sample
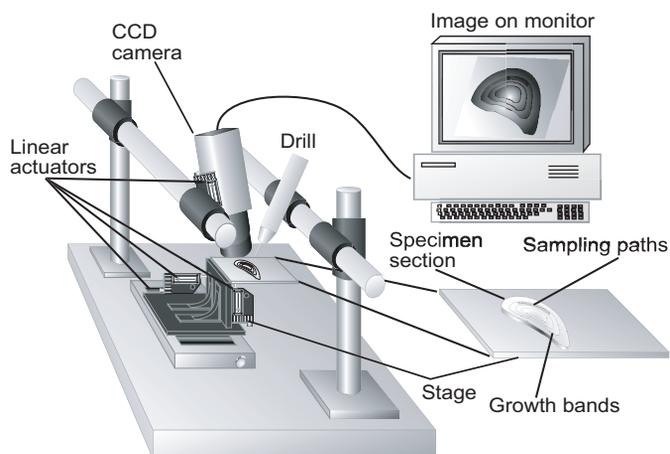
Figure 1. Schematic of micromilling apparatus. Specimen is attached underneath a fixed dental drill and viewed on large screen monitor via color digital camera. Computer-control drives motion controller via IEEE-488 interface, and permits stage manipulation in three directions via three micropositioning actuators (after Wurster et al., 1999).
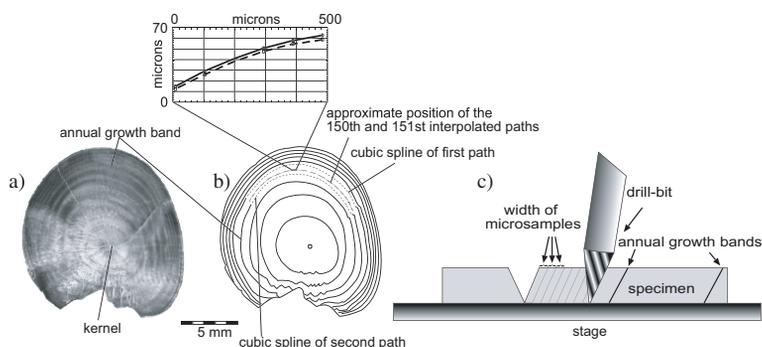

Figure 2. Illustration showing how carbonate is extracted from sample paths narrower than dental drill width. Note how first sample is coarsely drilled without extracting high-resolution time-specific carbonate. High-resolution samples are later extracted by milling carbonate from specimen using dental drill bit. Note micron-scale widths of subsequent sample paths (after Wurster et al., 1999).

path, and mass is calculated from the volume using the density of the sampled mineral. Current mass spectrometer technology using automated carbonate preparation systems for analysis usually requires $\sim 20\,\mu$g of carbonate. Although the length function is determined by the morphology of the specimen, manipulation of both depth and width functions is possible. The depth function is selected by increasing or decreasing the drill depth (z-axis). The width function is determined by the number of intermediate paths between any two digitized paths (the greater the number of intermediate sampling paths, the higher the resolution and the lower the sample size and mass). Carbonate samples are manually collected with a small scalpel while viewing the specimen on the large screen monitor. Each sample is stored in a stainless steel vessel, which is placed in numbered brass convoys prior to analysis.

Stable isotope values of lacustrine fish

As with $\delta^{18}O_{(PO_4)}$ values, application of $\delta^{18}O_{(CaCO_3)}$ values to paleotemperature requires that the $\delta^{18}O_{(H_2O)}$ value be determined. There are currently two methods for determining the $\delta^{18}O_{(H_2O)}$ value of ancient freshwater using mineral elements of fishes; micromilling of otoliths with specific thermal growth requirements (Patterson et al., 1993), paired-species analysis (Smith & Patterson, 1994), or a combination of the two techniques. Paired-species analysis uses a cold-water obligate benthic fish such as a deep-water sculpin (restricted to 4 °C) to obtain $\delta^{18}O_{(H_2O)}$ values. Once paleo-water $\delta^{18}O_{(H_2O)}$ values are constrained, warm water stenothermic and eurythermic species can be analyzed by micromilling to interpret seasonal variation in surface-water temperatures that are directly related to atmospheric conditions (Patterson et al., 1993; Patterson, 1998). If the eurythermic species has a minimum thermal tolerance for growth, the highest isotope value each year will represent carbonate precipitated the minimum growth temperature (Patterson et al., 1993; Smith & Patterson, 1994; Patterson 1998). For shallow-water species these water temperatures correspond to mean weekly atmospheric temperature (Patterson et al., 1993; Wurster & Patterson, 2000). Thus, shallow-water fish can provide a detailed record of atmospheric temperature for the past. The resolution obtainable from these structures is easily suitable for reconstructing paleoclimate in great detail. The recent advances are sufficient to generate records that essentially represent paleo-weather data.

Stable isotope evidence from river-dwelling fish

Fish remains recovered from rivers provide additional hydrological and climatological information while presenting a different challenge because $\delta^{18}O_{(H_2O)}$ values may vary to a greater degree than lakes on an intra- and inter-annual basis. The seasonal maximum $\delta^{18}O_{(CaCO_3)}$ value used to calculate $\delta^{18}O_{(H_2O)}$ may change each year, reflecting different sources and amounts of seasonal precipitation. For example, otoliths of freshwater drum (*Aplodinotus grunniens*) were micromilled and analyzed to determine $\delta^{18}O_{(H_2O)}$ values and summer maximum temperatures of the Holston River in Tennessee for the last 5,500 years (Wurster & Patterson, 2000). Significantly, it appears that this technique has the sensitivity to discern individual storm events if sufficient precipitation enters the watershed (Fig. 3). During the late Hypsithermal, summer temperatures were generally higher than in the modern and tropical storms have been proposed by models to be more frequent (Emanuel, 1987; Gutowski et al., 1994). In Figure 3, the late season apparent rise in temperature during year 4 is interpreted to represent tropical storm moisture that is known to have significantly lower $\delta^{18}O_{(H_2O)}$ values due to the high degree of distillation (e.g., Lawrence & Gedzelman, 1996). By examining otoliths through a sequence of sediment or rock, secular variation in temperature and $\delta^{18}O_{(H_2O)}$ values can be derived (Patterson, 1998; Wurster & Patterson, 2000). Figure 4 presents temperature and $\delta^{18}O_{(H_2O)}$ values for the South Fork of the Holston River in Tennessee, derived from a series of otoliths recovered from the Eastman rockshelter archaeological site at Eastman TN. Otoliths range in age from 5,500 to 300 years old. Oxygen isotope analysis should now permit tests of climatic hypotheses based on taxon habitat as the basis for inference (e.g., Smith, 1963; Shoshani & Smith, 1996), which are ambiguous because of the conflation of amount of water and temperature effects (Cross, 1970).
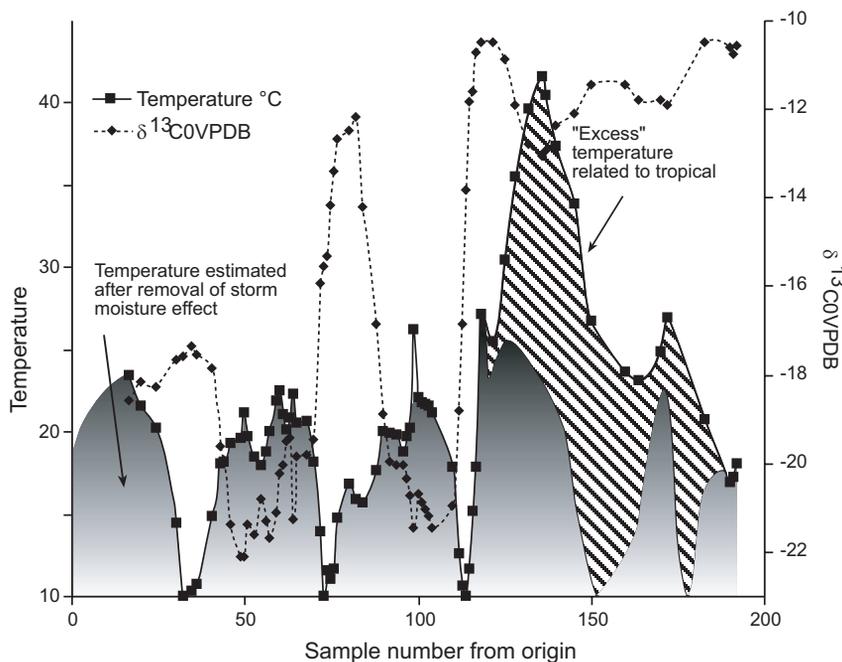
Figure 3. $\delta^{13}C_{(CaCO_3)}$ values and temperatures (calculated from $\delta^{18}O_{(CaCO_3)}$ values) from a 2,900-year-old Freshwater Drum otolith recovered from the Eastman Rockshelter archaeological site in Tennessee, USA. Samples represent a three-day resolution in temperature and metabolism. $\delta^{18}O_{(CaCO_3)}$ values have been converted to temperatures assuming that the highest $\delta^{18}O$ value each year represents carbonate precipitated at 10 °C. The apparent peak temperatures in year 4 are well above the thermal tolerance for this species. These values are interpreted to represent incursion of highly distilled tropical moisture during at least one storm event. $\delta^{13}C$ values which are predominately a function of metabolic rate do not indicate excessively high temperatures, thus we invoke a large decrease in $\delta D_{(H_2O)}$ value at the end of the summer (data from Wurster & Patterson, 2000).

Lake depth, salinity, oxygenation, temperature

Coldwater fish such as trout and whitefish are indicators of cool waters and possibly cold paleoclimate (Rogers et al., 1985, 1992; Firby et al., 1997). Ambiguity arises because coldwater fish are also indicators of water depth. Other indicators of depth–sediment texture, lack of scavenger action and other indicators of anoxia, and sedimentary context are sometimes difficult to interpret. Behavior of decaying carcasses may provide depth estimates when low temperatures, salinity, and (or) pressures constrain bacterial action (Allison et al., 1991). Fossil evidence of the nature of carcass decay and disturbance by scavengers is therefore an important link in connecting paleolimnological evidence to paleoclimate analysis.

Fish evidence for depth and sedimentation rates in the lake deposits of the Miocene Clarkia Formation, in the St. Maries River basin, Idaho, suggested conclusions different from those provided by plant fossils (Elder & Smith, 1985, 1988). Freshwater conditions were indicated by the fact that two of the taxa present are restricted to fresh water and warm climate was indicated by the restriction of one of the fish families present to warm
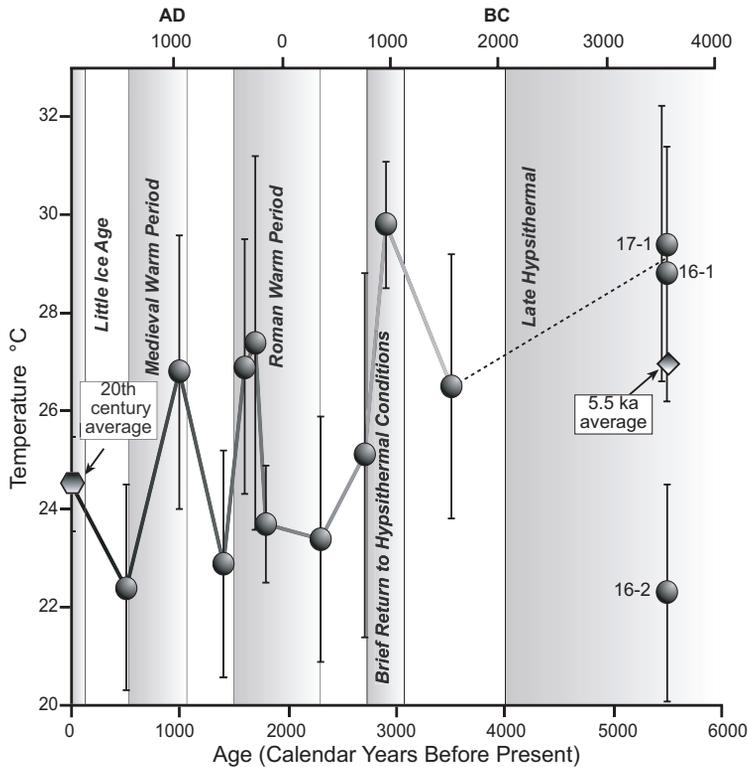
Figure 4. Estimated maximum summer temperature and average $\delta^{18}O_{(H_2O)}$ values from 5.5 ka to 0.3-1.0 ka derived from intra-otolith $\delta^{18}O_{(CaCO_3)}$ values of 14 sagittae recovered from the Eastman. Bars represent variation in estimated temperature using calculated $\delta^{18}O_{(H_2O)}$ +1‰ and are not representative of error. Twentieth-century average maximum temperature is plotted for comparison. Modern $\delta^{18}O_{(H_2O)}$ value (collected 3/24/99, at the approximate seasonal start of fish growth) is included for comparison (data from Wurster & Patterson, 2000).

waters. The evidence of minimal but observable scavenger action (by crayfish or snails) on decaying fish established occasional oxygenation to the lake bottom, despite the warm water habitat. Constraints on the depth of the lake were quantified by experimental work that established the relationship between pressure and temperature in the flotation of dead fish by bacterial decay gases. At temperatures above 16 °C, pressure equivalent to 10 m of water are required to keep bubbles of decay gases from accumulating and floating positively buoyant fish carcasses (Elder & Smith, 1985). Thus, application of fossil observations and laboratory experiments provides evidence for depth and temperature.

Mass mortality layers are assemblages of fossil organisms that died in a catastrophic event, as indicated by their concentration in a single stratum. The cause of death is usually anoxia or an increased concentration of CO_2 or decay gases released by turnover, or sudden temperature change. Combinations of ecological, taphonomic, and taxonomic interpretation are usually required. There is a limited signal indicating cause of death in the posture and decay pattern of the dead fish. Anoxia causes distended gill chambers and

concave-up distortion of the vertebral column. Scavenger disturbance indicates presence of oxygen; absence of scavengers indicates anoxia. Death assemblages also provide detailed information about limnological conditions of life and population dynamics (Wilson, 1980, 1988a, 1988b; Bell et al., 1989).

Exceptionally rich faunas may also contribute to chemical information. The diverse fish, mollusk, and ostracod faunas of the Pliocene Glenns Ferry Formation, Idaho, is represented by massive amounts of calcite, aragonite, and apatite, consistent with the presence of alkaline, but not saline, nutrient-rich conditions, confirmed by abundant biogenic oolite (Swirydczuk et al., 1979, 1980).

Rates of lacustrine sedimentation

Sedimentation rates are important to paleolimnological interpretation, but are sometimes controversial. Tree leaf chemistry and distinct sediment laminae (Smiley & Rember, 1985) in the Miocene Clarkia Formation, St Mary's drainage, Idaho, suggested rapid sedimentation in a small lake. Many species of tree leaves recovered from the formation are fresh in appearance (leaves and fish retain some original pigment and organic chemistry for a few moments after being exhumed; i.e., until oxidized), suggesting that burial was nearly instantaneous, in a storm event. However, fish taphonomy contradicts this conclusion (Elder & Smith, 1985). Long periods of slow decay in cold water, with minimal sedimentation and minimal scavenger action, are indicated by the presence of small fans or splays of scores of minute (1 mm) fin-ray bones, dispersed evenly across the bottom up to 4 cm away from the fins of the fishes by gentle currents after extensive decay. Slow decay and exposure to slow, unidirectional currents for several months are indicated by the graded dispersion of the fine bones (lepidotrichs). Laminar sediment couplets (presumably annual, on the basis of the above observations) are about 1 mm thick, further suggesting slow, gradual, sedimentation rates (Smith & Elder, 1985). Some sedimentary layers are penetrated by the decaying bodies of the fishes.

Lake vs. stream habitats

High vs. low energy environments are not always easily diagnosed because constraints on sediment sources do not permit the full range of clasts and sediment textures (Pickard & High, 1985). Lacustrine and low energy fluvial habitats may have identical sediment particle sizes. The first step in analysis is to determine the energy level in the local paleoenvironments; the lateral and vertical relations of these will point to lacustrine vs fluvial settings. Fish can help support inferences made on the basis of sediment textures. Lacustrine and low-energy habitats in general are indicated by fossils belonging to groups that live primarily in lakes (the method of taxonomic analogy) and also by presence of fish with a ratio of body depth to length exceeding 0.3, such as bluegill sunfish or other deep-bodied fish (the method of ecomorphology). Certain taxonomic groups are restricted to lowland lakes in modern settings, for example, catfish, sunfish, bass, perch, drum, or esocids that normally live in eastern North American lakes lower than 1200 m above sea level. It is probable that co-occurrence of fossil relatives of these groups indicates similar restriction (Lundberg & Smith, 1978; Smith et al., 2000), but this general method of inference, alone,

is weak because it ignores the possibility of change in physiology or behavior of the indicator organisms (Binford et al., 1985). Inferences about habitats are now testable by isotopic analysis and by the ecomorphological approach. The analysis of body shapes that function in restricted ecological settings (ecomorphology) has potential for providing tests of hypothesized low-energy waters. Just as large, smooth-margined leaves indicate moist tropical climates (Wolf, 1971), absence of deep-bodied fish from a community indicates high-energy environments. Deep-bodied sunfish, cichlids, pupfish, suckers, minnows, and characins, for example, inhabit low-elevation, low-energy environments (Perrine, 2000).

Elevation

The identification of relative elevation above sea level in the sedimentological record is problematical. It is especially difficult to determine whether a lake existed on a high plateau or a lowland, because the modern elevation of the sediments is not good evidence for the original elevation of the body of water. River sediments are easier if the broad lateral context of the basin is well known, but may be ambiguous. The problem may be approached as an issue of energy in the depositional system, similar to the analysis of above, because of the correlation between elevation, gradient, and current velocity. Fish may contribute to the solution to this problem because only slender fishes such as sculpins, darters, and trouts inhabit high-gradient streams. Deep-bodied fishes such as sunfish, bass, carp-suckers, buffalofish, carp, or cichlids inhabit low-gradient streams (with a mix of slender-bodied fishes). The occurrence of any of the deep-bodied fish in a fossil fauna indicates low gradients and elevations lower than 1200 m (Perrine & Smith, in prep.). A survey of modern fish habitats in the United States, Mexico, South America, and Madagascar indicates that deep-bodied, spiny-rayed fish such as sunfish and cichlids (Perciformes) are not naturally found above 1200 m in elevation (Perrine & Smith, in prep.). Hydrodynamic pressures on deep-bodied fish apparently eliminate them from swift currents. Therefore access to high elevation lakes as well as high elevation fluvial environments is eliminated.

   Exceptional cases of lakes and low-gradient rivers in basins perched at high elevations are possible, but these are especially short-lived in geological time, so time and high-gradient barriers in rivers interact to keep deep-bodied fishes from these environments. Such settings are usually inaccessible because they are separated from lowlands by downstream barriers of high gradient. Known cases of low gradients at high elevations, in low latitudes, such as the Peruvian and Bolivian Andes and Mexican Plateau, are not inhabited by deep-bodied, spiny-rayed fish.

Summary

Taphonomic and taxonomic data from fishes are used to identify physical, chemical, and ecological conditions in ancient environments.
1) Temperatures of ancient environments are estimated by oxygen isotopic ratios in aragonitic otoliths or apatite of bone, as well as by presence or absence of fish that belong to known warm-water or cold-water groups.
2) Analysis of the conditions of death, scavenger disturbance, and carcass decay may enable identification of cold, stratified lakes and estimation of oxygen, water chemistry,

and sedimentation patterns.

3) Climatic seasonality can be analyzed as temperatures recovered by isotopic analysis of aragonite or apatite growth rings representing different seasons. The growth bands in these accretionary structures are micromilled from growth rings and analyzed in a mass spectrometer.

4) Salinity is indicated by presence or absence of fish with narrow salinity tolerance (stenohaline) in contrast with fish that are broadly tolerant of salinity (euryhaline fish).

5) Migrations are determined by microsampling different years of life, as represented in oxygen isotopes in otoliths or bone, and recovering evidence of travel to distinctive chemical environments.

6) Current energy and elevation may be indicated by fish body-shapes and taxon-diagnostic adaptations. Deep-bodied fishes are restricted to waters with low current or wave energy.

7) Hydrographic connections, lake spillovers, and stream captures are indicated by biogeographic patterns of species distributions. Fish in adjacent but separate hydrographic basins indicate former continuous fish habitat between the basins.

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