Notes

Precision of Structures Used to Estimate Age and Growth of Apache Trout from Arizona

Michael C. Quist,* Marta E. Ulaski, Kristy M. Manuell, Zachary J. Jackson, Tim Gatewood

M.C. Quist
U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, 875 Perimeter Drive MS 1141, Moscow, Idaho 83844

M.E. Ulaski
Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, 875 Perimeter Drive MS 1141, Moscow, Idaho 83844

K.M. Manuell, Z.J. Jackson
U.S. Fish and Wildlife Service, Arizona Fish and Wildlife Conservation Office, P.O. Box 39, Pinetop, Arizona 85935

T. Gatewood
White Mountain Apache Tribe Game and Fish Department, P.O. Box 220, Whiteriver, Arizona 85941

Abstract

Obtaining reliable information on the age structure of fish populations is important for making conservation and management decisions. We sought to evaluate precision and reader confidence in age estimates from scales (two body locations), sectioned fin rays (pectoral, pelvic, anal), and sectioned sagittal otoliths from Apache Trout *Oncorhynchus apache* ($n = 78$ fish) sampled from the East Fork White River, Arizona, in 2017. Two experienced readers without prior knowledge of fish length aged structures independently. Each reader provided a confidence rating of 0 (no confidence) to 3 (completely confident) as a measure of readability. Both readers were unable to estimate age from scales collected from the area just posterior to the insertion of the pectoral fin. We used scales removed from an area just dorsal to the lateral line and posterior to the dorsal fin in all analyses. Percentage of exact agreement between readers was highest for scales and otoliths (>72.0%) and lowest for fin rays (31.8–58.1%). Average confidence rating was highest for sectioned otoliths (mean ± SE, 2.1 ± 0.07), and lowest for anal fin rays (0.3 ± 0.06) and scales (0.7 ± 0.05). We compared consensus ages from otoliths to the other structures. Percentage of exact agreement with otolith age was low and varied from 21.6 to 35.7% among structures. Similarly, percentage of agreement within 1 y was also low among structures (58.0–70.2%). Scales consistently underestimated age of age-4 and older fish (based on otolith age), whereas fin rays tended to overestimate age of younger fish and underestimate age of older Apache Trout. Although sectioned otoliths require lethal sampling, they produced the most precise age estimates for Apache Trout with the highest reader confidence. Dorsal scales may be a suitable nonlethal alternative to otoliths if ages for only young fish (age 3 and younger) meet study objectives.

Keywords: age; growth; structure; otolith; scale

Received: March 2022; Accepted: March 2023; Published Online Early: April 2023; Published: June 2023

Citation: Quist MC, Ulaski ME, Manuell KM, Jackson ZJ, Gatewood T. 2023. Precision of structures used to estimate age and growth of apache trout from Arizona. *Journal of Fish and Wildlife Management* 14(1):188–194; e1944-687X. https://doi.org/10.3996/JFWM-22-021

* Corresponding author: mcquist@uidaho.edu

Introduction

The Apache Trout *Oncorhynchus apache* is endemic to streams in the White Mountains of east-central Arizona and represents one of the southernmost species of *Oncorhynchus*. Although populations are present in high-elevation streams in the Black, White, and Little Colorado river drainages (Miller 1972), they now occupy about 281 km of streams instead of the estimated 965–1,320 km they once occupied (USFWS 2009, 2022). The White Mountain Apache Tribe first recognized declining Apache Trout populations in the late 1940s, and attempted to protect remaining populations by implementing fishing prohibitions and protecting important habitats during the 1950s (USFWS 1979). A variety of factors contributed to the decline of Apache Trout, including the introduction of nonnative salmonids, extensive habitat alteration, and overexploitation. Interactions (i.e., competition, predation) with nonnative Brown Trout *Salmo trutta* and Brook Trout *Salvelinus fontinalis* led to widespread declines of Apache Trout, and hybridization with Rainbow Trout *Oncorhynchus mykiss* and Cutthroat Trout *Oncorhynchus clarkii* reduced the distribution of genetically pure Apache Trout (Rinne and Minckley 1985; Carmichael et al. 1993). Timber harvest, livestock grazing, and water development have also had detrimental effects on Apache Trout habitat. Primary effects from these alterations include changes to riparian corridors and streambank morphology, altered hydrology and thermal characteristics, reduced quantity and quality of spawning habitat, and reduced production of macroinvertebrates (USFWS 2009). Initial federal protections for the species came along with listing as endangered under the U.S. Endangered Species Preservation Act in 1967 (USFWS 1967, 2022). Apache Trout were subsequently downlisted as threatened under the U.S. Endangered Species Act (ESA 1973, as amended) in 1975 due to the discovery of additional populations, successful captive culturing, removal of overexploitation as a threat, and reduction of logging and hybridization as threats (USFWS 1975, 2022). The U.S. Fish and Wildlife Service (USFWS) released the first Apache Trout Recovery Plan in 1979, with revisions in 1983 and 2009 (USFWS 1979, 2009).

Recovery objectives are not a statutory requirement of recovery plans, but wildlife managers often develop them to define the outcome that they intend recovery actions to accomplish. The recovery objective for Apache Trout is to establish and maintain 30 self-sustaining discrete populations of pure Apache Trout within its historical range (USFWS 2009). A detailed discussion on the merits of the recovery objectives is beyond the scope of this paper. However, assessing the occurrence and extent of self-sustaining Apache Trout populations is reliant on obtaining information on their population demographics and dynamics. For instance, a self-sustaining population implies the presence of periodic reproduction and multiple age classes (e.g., Allen and Hightower 2010). Age estimation is a fundamental component of fish population assessments and provides the foundation for estimating other rate functions (e.g., growth, recruitment, mortality). With regard to Apache Trout, understanding the age structure and dynamic of populations is important for informing decisions during the ongoing recovery process and managing populations into the future. Information on age structure, coupled with information on growth and mortality, is also important for better understanding the ecology of Apache Trout and their response to management and conservation actions regardless of their listing status.

The most frequently used technique to estimate fish age involves using calcified or hard structures (Quist et al. 2012). Cleithra, scales, otoliths, spines, and fin rays are among the hard structures commonly used for age estimation with the most reliable structure often varying among species and geographic location (Maceina et al. 2007; Branigan et al. 2019). When choosing a structure for age and growth analysis, scientists must consider a variety of factors such as lethality involved with structure extraction and whether the structure provides precise and accurate age estimates (Phelps et al. 2017). For example, otoliths consistently provide accurate age estimates, but they are time consuming to process and require sacrificing fish (Isermann et al. 2003; Long and Grabowski 2017). Nonlethal structures (e.g., scales, fin rays, spines) may be preferred for species of high conservation concern where any additional mortality must be avoided (Quist et al. 2012; Phelps et al. 2017).

Investigations on the age and growth of Apache Trout are limited to two studies. Harper (1976) collected otoliths from 37 Apache Trout in the headwaters of Big Bonito Creek, Arizona, to estimate age and growth. Kitcheyan (1999) used scales to estimate age of Apache Trout from two creeks in Arizona. However, no research has evaluated precision of ageing structures for Apache Trout. Identifying which hard structures provide the most replicable age estimates with the highest level of confidence should lead to improved estimates of population rate functions and better inform management decisions. Identifying whether a nonlethal structure provides reliable age estimates would be particularly useful.

Given the conservation status of Apache Trout, sacrificing fish specifically for comparing structures is not feasible. However, fisheries managers brought wild Apache Trout from the East Fork White River, Arizona, into a hatchery with the goal of incorporating genetics from wild fish into the hatchery broodstock program. While in captivity, an accident killed 78 of the wild fish, thereby presenting an opportunity to evaluate the use of hard structures for ageing. The objective of this study was to evaluate the precision and readability of scales (two body locations), sectioned fin rays (pectoral, pelvic, anal), and sectioned sagittal otoliths for estimating age of Apache Trout.

Methods

The East Fork White River is located on the Fort Apache Indian Reservation, Arizona, and contains a population of wild, genetically pure Apache Trout. The East Fork White River is a high-elevation, high-gradient

system located on the southwestern slope of Mount Baldy. Apache Trout is the only fish species present and the fish occur in an ~8.2-km stretch of river located upstream of a natural barrier.

Staff from the White Mountain Apache Tribe Game and Fish Department, Arizona Fish and Wildlife Conservation Office, and Alchesay-William Creek National Fish Hatchery Complex sampled Apache Trout from the East Fork White River in October 2017 with a backpack electrofisher. Individuals greater than 100 mm were collected ($n = 100$) and transported to Williams Creek National Fish Hatchery, Arizona. The Williams Creek Hatchery is spring fed with a near constant water temperature around 11°C. Hatchery staff held the fish for approximately 6 mo, then examined them for indications of sex, measured them to the nearest millimeter (total length), weighed them to the nearest gram, and implanted them with a passive integrated transponder tag. After 10 mo in the hatchery (August 8, 2018), all remaining fish died when a water supply that was thought to be unconnected to the quarantine facility was treated with chlorine. Hatchery staff froze the fish, which were later flown to the University of Idaho for age and growth analyses.

We measured total length of individual fish to the nearest millimeter. We removed scales from two locations: 1) just posterior to the insertion of the pectoral fin (hereafter pectoral scales) and 2) dorsal to the lateral line and just posterior to the dorsal fin (hereafter dorsal scales; Quist et al. 2012). We removed scales with the tip of a knife, placed them onto a folded piece of paper that was inserted into a coin envelope, and allowed them to air dry (McInerny 2017). Once dry, we separated scales and pressed between two glass microscope slides that we taped at each end. We removed the marginal pectoral, pelvic, and anal fin rays with scissors at the articulation of the fin ray with the body wall following the procedure outlined in Koch et al. (2008). We placed fin rays into labeled coin envelopes and allowed them to dry. We then mounted fin rays in epoxy following Koch and Quist (2007) and cross-sectioned (~0.8 mm thick) with a Buehler Isomet low-speed saw (Buehler, Lake Bluff, IL). We removed sagittal otoliths following Schneidervin and Hubert (1986). We stored otoliths in a microcentrifuge tube that we placed in a coin envelope. We placed a small mark on the nucleus of the otolith using a micropen to ensure that cross-sections included the nucleus. We mounted otoliths in epoxy and sectioned (~1.3 mm thick) in the dorsoventral plane (Quist et al. 2012; Long and Grabowski 2017). Although sectioned otoliths take more time to process than whole otoliths (e.g., Isermann et al. 2003), sectioned otoliths regularly provide more accurate and precise age estimates than whole otoliths (e.g., Hyndes et al. 1992; Newman et al 2000; Gallagher et al. 2016). We polished fin ray and otolith sections with progressively finer abrasive paper until additional efforts failed to improve clarity. We used an image analysis system consisting of a stereoscope coupled to a computer using image analysis software (Image Pro-Plus; Media Cybernetics, Rockville, MD) to read the structures.

Two readers independently enumerated annuli on each hard structure. Both readers had extensive experience ageing fishes using a variety of structures from a diversity of fish species and geographic locations. Readers had no prior knowledge of fish length or age estimates from other structures. Each reader estimated an initial age independently and assigned a confidence rating from 0 to 3. A confidence rating of 0 indicated that the reader had no confidence in their age estimate and a rating of 3 indicated high confidence (Koch et. al 2008; Spiegel et al. 2010). After each reader estimated age for a given structure, they compared presumptive ages. If age estimates differed, readers would discuss the structure until they reached a consensus age. If they could not reach a consensus age, we removed the structure from further analyses.

We used age-bias plots to evaluate between-reader and between-structure (i.e., consensus age) precision (Campana et al. 1995; Buckmeier et al. 2017). We conducted between-structure comparisons in relation to sectioned otoliths. We calculated percentage of exact agreement (PA) and percentage of agreement within 1 y (PA-1) between readers and structures. We also calculated the coefficient of variation (CV = [SD/mean] × 100) as an additional estimate of precision in age estimates between readers and structures (Campana et al. 1995).

Results

We estimated ages for 78 Apache Trout varying in total length from 113 to 235 mm (mean ± SD, 169.9 ± 33.7 mm; Data S1, *Supplemental Material*). Both readers deemed several structures from individual fish unreadable. We removed pectoral scales from the analysis because they were exceptionally small and both readers had no confidence in age estimates using the structure. They reached a consensus age for all remaining structures. This resulted in the use of samples from 77 fish for dorsal scales, 75 for otoliths, 74 for pectoral fin rays, 67 for pelvic fin rays, and 44 fish for anal fin rays. Consensus age estimates varied from 1 to 5 y for scales, 2 to 6 y for anal fin rays, 2 to 8 y for pectoral fin rays, and 2 to 9 y for pelvic fin rays and otoliths.

We first compared estimated ages for each of the ageing structures between the two readers. Percentage of exact agreement between readers was highest for dorsal scales (72.7%) and otoliths (72.0%), and lowest for pelvic (58.1%), pectoral (54.0%), and anal fin rays (31.8%; Figure 1). We observed similar patterns for PA-1 with the highest agreement observed for dorsal scales and otoliths (>96.0%), and lowest agreement for fin rays (<90%). The between-reader CV was lowest for otoliths (5.1) and highest for anal fin rays (16.9; Figure 1).

We compared consensus age estimates across structures to provide additional insight on variability among ageing structures. When compared to sectioned otoliths, percentage of agreement was generally low among structures (Figure 2). Percentage of exact agreement with otolith ages was highest for pelvic fin rays (35.7%), anal fin rays had the best agreement within 1 y (70.2%). Scales exhibited the lowest agreement (PA = 21.6%; PA-1

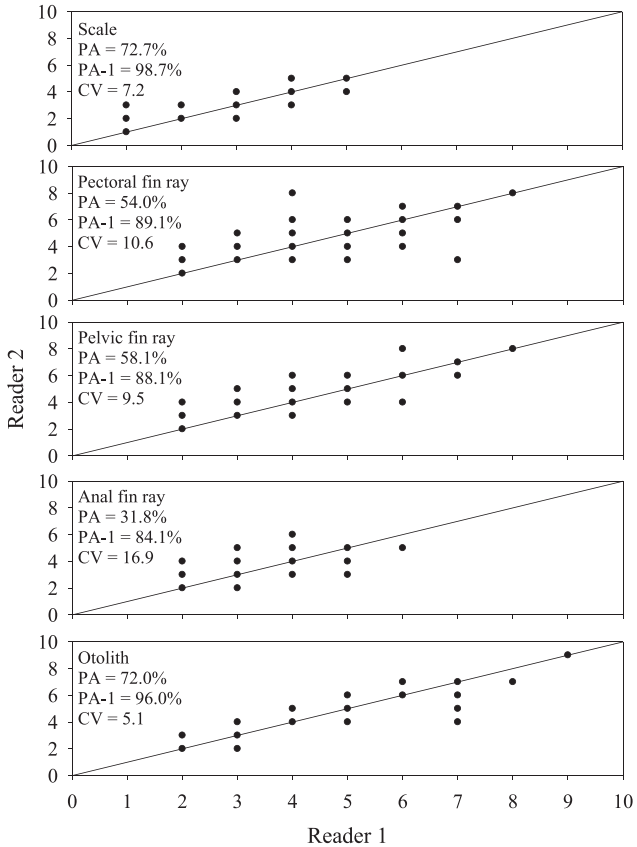

Figure 1. Comparison of reader age estimates from dorsal scales, fin rays (pectoral, pelvic, anal), and sectioned otoliths from Apache Trout *Oncorhynchus apache* sampled from the East Fork White River, Arizona, in 2017. Percentage of exact agreement (PA), percentage of agreement within 1 y (PA-1), and the coefficient of variation (CV) are provided as measures of precision.

= 58.0%) with otolith ages. Pectoral fin rays had the lowest CV (Figure 2).

Reader 2 was generally more confident in their age estimates than reader 1 (Figure 3). Across readers, confidence was highest for otoliths (mean ± SE, 2.1 ± 0.07) and low for the other structures. The readers reported the lowest confidence for anal fin rays (0.3 ± 0.06) and scales (0.7 ± 0.05).

Discussion

Researchers have not validated annulus formation on hard structures for Apache Trout and, therefore, our research can only provide insight on precision of different structures. However, sagittal otoliths have repeatedly been shown to provide accurate age estimates for a variety of fishes, including salmonids (e.g., Haglund and Mitro 2017; Phelps et al. 2017; Branigan et al. 2019). For instance, Hining et al. (2000) validated annulus formation in Rainbow Trout from southern Appalachian streams and Schill et al. (2010) validated otoliths for ageing Redband Trout *Oncorhynchus mykiss gairdneri* in high desert streams in southwestern Idaho.

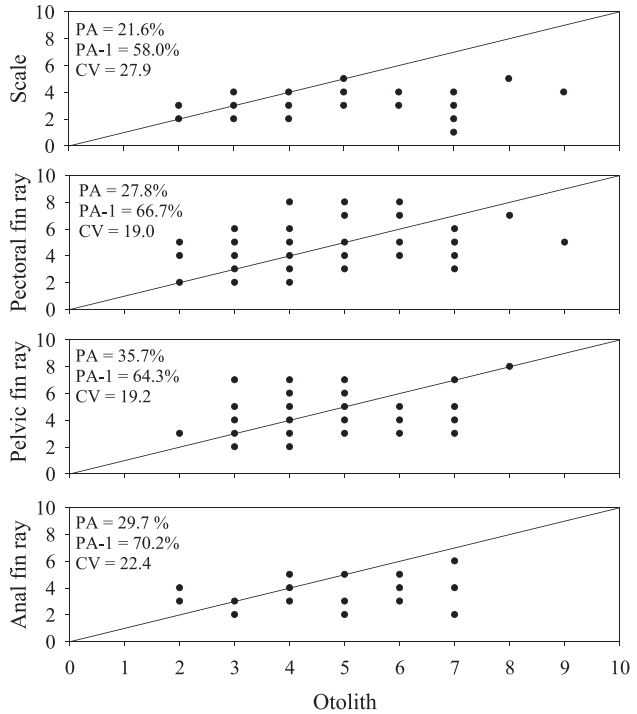

Figure 2. Comparison of consensus ages from dorsal scales and fin rays (pectoral, pelvic, anal) with sectioned otoliths from Apache Trout *Oncorhynchus apache* sampled from the East Fork White River, Arizona, in 2017. Percentage of exact agreement (PA), percentage of agreement within 1 y (PA-1), and the coefficient of variation (CV) are provided as measures of precision.

Other researchers have shown otoliths to provide accurate age estimates for Arctic Grayling *Thymallus arcticus* in Alaska (DeCicco and Brown 2006) and for Chinook Salmon *Oncorhynchus tshawytscha* along the Pacific coast of Canada (Murray 1994). Although we were

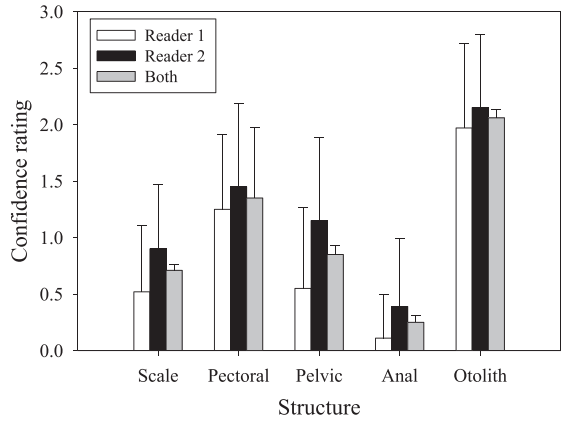

Figure 3. Mean reader confidence ratings for age estimates from dorsal scales, fin rays (pectoral, pelvic, anal), and sectioned otoliths from Apache Trout *Oncorhynchus apache* sampled from the East Fork White River, Arizona, in 2017. Ratings varied from 0 (no confidence) to 3 (high confidence). Error bars represent one standard deviation for readers and one standard error for the overall mean (i.e., both).

unable to validate otolith ages in our study, sectioned otoliths yielded the most readable (i.e., highest confidence rating) and precise age estimates compared to the other structures.

Scales are traditionally the most common structure used to age fishes (Quist et al. 2012; McInerny 2017). Studies have shown scales to provide accurate and precise age estimates for some species, but they seem to perform best for young fish, fast-growing fish, and in systems with high seasonal variation in temperature or prey resources (McInerny 2017; Phelps et al. 2017). Unfortunately, scales regularly underestimate the age of fishes. For example, DeCicco and Brown (2006) found that scales underestimated age of Arctic Grayling by as much as 20 y in an Alaskan river system. Hining et al. (2000) found that scales were inaccurate for age-3 and older Rainbow Trout in Tennessee and North Carolina. Schill et al. (2010) reported that scales underestimated age and were unreliable for Redband Trout in Idaho. Between-reader precision was high for scales sampled from Brook Trout in West Virginia streams, but they underestimated age of age-3 and older fish compared with otoliths (Stolarski and Hartman 2008). Similar results have been reported for a diversity of trout and char (e.g., Kruse et al. 1997; Mogen and Kaeding 2005; Zymonas and McMahon 2009; Erhardt and Scarnecchia 2013). In our study, scales provided relatively high between-reader precision compared to the other structures, including otoliths. However, scales tended to underestimate age of age-3 and older Apache Trout (i.e., based on consensus otolith age) by up to 6 y. When either reader had zero confidence in a scale age, PA was 50.0% and PA-1 was 100% for age-3 and younger Apache Trout (i.e., based on consensus otolith age). When both readers had a confidence rating equal or greater than 1, PA was 45.5% and PA-1 was 100% for the same group of fish. Assuming that otoliths provide reasonably accurate age estimates, scales may provide useful age estimates for age-3 and younger Apache Trout. Unfortunately, the age distribution of fish limits our study in that only 23 age-3 and younger fish were available for study. Additional research would provide further insight on the application of ageing scales for young Apache Trout.

Fin rays are nonlethal structures that have produced mixed results depending on the species and system. In some systems, fin rays provide age estimates that are accurate and concordant with otolith ages. Copeland et al. (2007) found that dorsal fin rays were nearly 99% accurate in estimating age of known-age Chinook Salmon in Idaho. Pelvic fin rays were 88% accurate for Bull Trout *Salvelinus confluentus* in Idaho and Montana streams (Zymonas and McMahon 2009). Erhardt and Scarnecchia (2013) also evaluated pelvic fin rays from Bull Trout and found that they performed well for fish in the North Fork Clearwater River system, Idaho. In contrast to these studies, other research has reported low precision and accuracy from salmonid fin rays. Pectoral fin rays from Brook Trout in West Virginia provided age estimates with low between-reader precision (Stolarski and Hartman 2008). Hubert et al. (1987) found that dorsal and pectoral fin rays underestimated ages compared with otoliths from Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouveri* in Yellowstone Lake. Gallagher et al. (2016) reported that pectoral and pelvic fin rays underestimated age for age-5 and older Dolly Varden *Salvelinus malma* from the Canadian arctic. Of the different fin rays examined in our study, reader confidence was highest for pectoral fin rays, but all fin rays had poor between-reader precision and rarely agreed with otolith ages. Unlike scales, which tended to underestimate age, fin rays appeared to overestimate age at early ages and underestimate age at older ages.

A potential factor influencing the patterns observed in our study was that fish were in a hatchery for almost a year. We did not notice any obvious issues with interpreting structures that captive rearing could have caused. In addition, a single year of atypic growth cannot explain the magnitude of error observed in our study. Nevertheless, our results suggest that scales may provide useful age estimates for fish younger than age 4 but are unreliable thereafter. Similarly, fin rays tended to provide age estimates that were inconsistent between readers and with otolith ages. Otoliths appear to be the most precise structure for the full range of Apache Trout ages. Future efforts focused on other Apache Trout populations (e.g., opportunistic samples from field mortalities) with a wide range of ages and validating structures for ageing would be particularly helpful.

Acknowledgments

We thank Jennifer Johnson, Chad Baumler, Rob Bettaso, Inez Billy, Mike Figueroa, Justin Gatewood, Isaiah Paxson, Gene Okamoto, and Jonathan Walker for assistance with field collection of the fish used in this study. Zach Beard and two anonymous reviewers provided helpful comments on a previous version of this manuscript. We recognize the White Mountain Apache Tribe for their distinguished commitment to Apache Trout conservation and management and thank them for their support and authorization to pursue publishing this work. Additional support for this work was provided by the U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, which is jointly sponsored by the University of Idaho, U.S. Geological Survey, Idaho Department of Fish and Game, and Wildlife Management Institute.

Any use of trade, product, website, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Raw data, including fish identification number, total length (mm), age estimates for each reader, confidence ratings for each reader, and consen-

sus age estimate by ageing structure for Apache Trout *Oncorhynchus apache* sampled from the East Fork White River, Arizona, in 2017.

Available: https://doi.org/10.3996/JFWM-22-021.S1 (61 KB XLSX)

Reference S1. [ESA] U.S. Endangered Species Act of 1973, as amended, Pub. L. No. 93-205, 87 Stat. 884 (Dec. 28, 1973).

Available: https://doi.org/10.3996/JFWM-22-021.S2 (228 KB PDF) and https://www.fws.gov/endangered/esa-library/pdf/ESAall.pdf

Reference S2. [USFWS] U.S. Fish and Wildlife Service. 1967. Federal Register 32:48(11 March 1967):4001.

Available: https://doi.org/10.3996/JFWM-22-021.S3 (8.490 MB PDF)

Reference S3. [USFWS] U.S. Fish and Wildlife Service. 1975. Threatened status for three species of trout. Federal Register 40:137(16 July 1975):29863–29864.

Available: https://doi.org/10.3996/JFWM-22-021.S4 (37.455 MB PDF)

Reference S4. [USFWS] U.S. Fish and Wildlife Service. 1979. Recovery plan for Arizona trout, *Salmo apache*, Miller, 1972. Albuquerque, New Mexico: USFWS.

Available: https://doi.org/10.3996/JFWM-22-021.S5 (1.267 MB PDF)

Reference S5. [USFWS] U.S. Fish and Wildlife Service. 2009. Apache Trout recovery plan. Second revision. Albuquerque, New Mexico: USFWS.

Available: https://doi.org/10.3996/JFWM-22-021.S6 (140 KB PDF)

Reference S6. [USFWS] U.S. Fish and Wildlife Service. 2022. Species Status Assessment for the Apache Trout *Oncorhynchus apache*. Flagstaff, Arizona: USFWS.

Available: https://doi.org/10.3996/JFWM-22-021.S7 (19.023 MB PDF)

References

Allen MS, Hightower JE. 2010. Fish population dynamics: mortality, growth, and recruitment. Pages 43–79 in Hubert WA, Quist MC, editors. Inland fisheries management in North America. 3rd edition. Bethesda, Maryland: American Fisheries Society.

Branigan PR, Meyer KA, Wahl NC, Corsi MP, Dux AM. 2019. Accuracy and precision of age estimates obtained from three calcified structures for known-age kokanee. North American Journal of Fisheries Management 39:498–508.

Buckmeier DL, Sakaris PC, Schill DJ. 2017. Validation of annual and daily increments in calcified structures and verification of age estimates. Pages 33–79 in Quist MC, Isermann DA, editors. Age and growth of fishes: principles and techniques. Bethesda, Maryland: American Fisheries Society.

Campana SE, Annanad MC, McMillan JI. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131–138.

Copeland T, Hyatt MW, Johnson J. 2007. Comparison of methods used to age spring-summer Chinook Salmon in Idaho: validation and simulated effects on estimated age composition. North American Journal of Fisheries Management 27:1393–1401.

DeCicco AL, Brown RJ. 2006. Direct validation of annual growth increments on sectioned otoliths from adult Grayling and a comparison of otolith and scale ages. North American Journal of Fisheries Management 26:580–586.

Erhardt JM, Scarnecchia DL. 2013. Precision and accuracy of age and growth estimates based on fin rays, scales, and mark-recapture information for migratory Bull Trout. Northwest Science 87:307–316.

Gallagher CP, Howland KL, Wastle RJ. 2016. A comparison of different structures and methods for estimating age of northern-form Dolly Varden *Salvelinus malma malma* from the Canadian Arctic. Polar Biology 39:1257–1265.

Haglund JM, Mitro MG. 2017. Age validation of Brown Trout in Driftless Area streams in Wisconsin using otoliths. North American Journal of Fisheries Management 37:829–835.

Harper KC. 1976. On the biology of *Salmo apache* and its management implications. Master's thesis. Tucson: University of Arizona. Available: https://repository.arizona.edu/bitstream/handle/10150/566616/AZU_TD_BOX291_E9791_1976_276.pdf?sequence=1 (March 2023)

Hining KJ, West L, Kulp MA, Neubauer AD. 2000. Validation of scales and otoliths for estimating age of Rainbow Trout from southern Appalachian streams. North American Journal of Fisheries Management 20:978–985.

Hubert WA, Baxter GT, Harrington M. 1987. Comparison of age determinations based on scales, otoliths, and fin rays for cutthroat trout from Yellowstone Lake. Northwest Science 61:32–36.

Hyndes GA, Loneragan NR, Potter IC. 1992. Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the Flathead *Platycephalus speculator*. Fishery Bulletin 90:276–284.

Isermann DA, Meerbeek JR, Scholten GD, Willis DW. 2003. Evaluation of three different structures used for Walleye age estimation with emphasis on removal and processing times. North American Journal of Fisheries Management 23:625–631.

Kitcheyan DC. 1999. Population structure of Apache Trout (*Oncorhynchus apache*) in Flash and Squaw creeks on the Fort Apache Indian Reservation, Arizona. Master's thesis. Tucson: University of Arizona. Available: https://www.proquest.com/openview/88e0c08

923e2d5ff5391fdf41c8cc7b2/1?pq-origsite=gscholar&cbl=18750&diss=y (March 2023)

Koch JD, Quist MC. 2007. A technique for preparing fin rays and spines for age and growth analysis. North American Journal of Fisheries Management 27:782–784.

Koch JD, Schreck WJ, Quist MC. 2008. Standardized removal and sectioning locations for Shovelnose Sturgeon fin rays. Fisheries Management and Ecology 15:139–145.

Kruse CG, Hubert WA, Rahel FJ. 1997. Using otoliths and scales to describe age and growth of Yellowstone Cutthroat Trout in a high-elevation stream system, Wyoming. Northwest Science 71:30–36.

Long JM, Grabowski TB. 2017. Otoliths. Pages 189–219 in Quist MC, Isermann DA, editors. Age and growth of fishes: principles and techniques. Bethesda, Maryland: American Fisheries Society.

Maceina MJ, Boxrucker J, Buckmeier DL, Gangl RS, Lucchesi DO, Isermann DA, Jackson JR, Martinez PJ. 2007. Current status and review of freshwater fish ageing procedures used by state and provincial fisheries agencies with recommendations for future direction. Fisheries 32:329–340.

McInerny MC. 2017. Scales. Pages 127–158 in Quist MC, Isermann DA, editors. Age and growth of fishes: principles and techniques. Bethesda, Maryland: American Fisheries Society.

Miller RR. 1972. Classification of the native trouts of Arizona with the description of a new species, *Salmo apache*. Copeia 1972:401–422.

Mogen JT, Kaeding LR. 2005. Identification and characterization of migratory and nonmigratory Bull Trout populations in the St. Mary River drainage, Montana. Transactions of the American Fisheries Society 134:841–852.

Murray CB. 1994. A method for preparing Chinook Salmon otoliths for age determination, and evidence of its validity. Transactions of the American Fisheries Society 123:358–367.

Newman SJ, Cappo M, Williams DM. 2000. Age, growth, mortality rates and corresponding yield estimates using otoliths of the tropical Red Snappers, *Lutjanus erythropterus*, *L. malabaricus* and *L. sebae*, from the central Great Barrier Reef. Fisheries Research 48:1–14.

Phelps QE, Tripp SJ, Hamel MJ, Koenigs RP, Jackson ZJ. 2017. Choice of structure for estimating fish age and growth. Pages 81–105 in Quist MC, Isermann DA, editors. Age and growth of fishes: principles and techniques. Bethesda, Maryland: American Fisheries Society.

Quist MC, Pegg MA, DeVries DR. 2012. Age and growth. Pages 667–731 in Murphy BR, Willis DW, editors. Fisheries techniques. 3rd edition. Bethesda, Maryland: American Fisheries Society.

Rinne JJ, Minckley WL. 1985. Patterns in variation and distribution of Apache Trout (*Oncorhynchus apache*) relative to co-occurrence with introduced salmonids. Copeia 1985:985–292.

Schill DJ, Mamer ERJM, LaBar GW. 2010. Validation of scales and otoliths for estimating age of Redband Trout in high desert streams of Idaho. Environmental Biology of Fishes 89:319–332.

Schneidervin RW, Hubert WA. 1986. A rapid technique for otolith removal from salmonids and catostomids. North American Journal of Fisheries Management 6:287.

Spiegel JR, Quist MC, Morris JE. 2010. Precision of scales and pectoral fin rays for estimating age of Highfin Carpsucker, Quillback Carpsucker, and River Carpsucker. Journal of Freshwater Ecology 25:271–278.

Stolarski JT, Hartman KJ. 2008. An evaluation of the precision of fin ray, otolith, and scale age determinations for Brook Trout. North American Journal of Fisheries Management 28:1790–1795.

[ESA] U.S. Endangered Species Act of 1973, as amended, Pub. L. No. 93-205, 87 Stat. 884 (Dec. 28, 1973). Available: https://www.fws.gov/endangered/esa-library/pdf/ESAall.pdf (see *Supplemental Material*, Reference S1).

[USFWS] U.S. Fish and Wildlife Service. 1967. Federal Register 32:48(11 March 1967):4001 (see *Supplemental Material*, Reference S2).

[USFWS] U.S. Fish and Wildlife Service. 1975. Threatened status for three species of trout. Federal Register 40:137(16 July 1975):29863–29864 (see *Supplemental Material*, Reference S3)

[USFWS] U.S. Fish and Wildlife Service. 1979. Recovery plan for Arizona trout, *Salmo apache*, Miller, 1972. Albuquerque, New Mexico: USFWS (see *Supplemental Material*, Reference S4).

[USFWS] U.S. Fish and Wildlife Service. 2009. Apache Trout recovery plan. Second revision. Albuquerque, New Mexico: USFWS (see *Supplemental Material*, Reference S5).

[USFWS] U.S. Fish and Wildlife Service. 2022. Species Status Assessment for the Apache Trout *Oncorhynchus apache*. Flagstaff, Arizona: USFWS (see *Supplemental Material*, Reference S6).

Zymonas ND, McMahon TE. 2009. Comparison of pelvic fin rays, scales and otoliths for estimating age and growth of Bull Trout, *Salvelinus confluentus*. Fisheries Management and Ecology 16:155–164.