

Articles

Validating a Nonlethal Method of Aging Endangered Juvenile Lost River and Shortnose Suckers

Barbara A. Martin,* Summer M. Burdick, Rachael K. Paul-Wilson, Ryan J. Bart

U.S. Geological Survey, Western Fisheries Research Center, Klamath Falls Field Station, 2795 Anderson Avenue, Suite 106, Klamath Falls, Oregon 97603

Present address of S.M. Burdick: U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, 5501A Cook-Underwood Road, Cook, Washington 98605

Present address of R.J. Bart: U.S. Fish and Wildlife Service, IFWO-Coeur d'Alene, 3232 W. Nursery Road, Coeur d'Alene, Idaho 83815

Abstract

Populations of imperiled Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers in Upper Klamath Lake, Oregon, are experiencing long-term decreases in abundance due to limited recruitment of juvenile suckers into the adult populations. Researchers use estimated ages based on fin rays to study environmental factors affecting year-class formation, generate annual juvenile sucker survival indices, and study variations in early life history. Biased or imprecise age estimates can lead to erroneous conclusions and have implications for age-based survival estimates, indications of recruitment, and growth estimators. We examined fin rays collected from individual suckers captured on multiple occasions and determined that juvenile suckers deposit a translucent increment on fin rays annually. Size-at-age data for suckers first captured as young as age 0 corroborated our finding of annual increment formation and indicate that the first increments are formed at age 1. We used edge and marginal increment analysis conducted on fin rays to determine the timing of annual increment formation. Our results indicate that increment formation occurs on fin rays of juvenile suckers from October to May and peaks between February and April.

Keywords: fin rays; Lost River sucker; shortnose sucker

Received: June 2022; Accepted: December 2022; Published Online Early: January 2023; Published: June 2023

Citation: Martin BA, Burdick SM, Paul-Wilson RK, Bart RJ. 2023. Validating a nonlethal method of aging endangered juvenile Lost River and Shortnose suckers. *Journal of Fish and Wildlife Management* 14(1):121–134; e1944-687X. <https://doi.org/10.3996/JFWM-22-039>

Copyright: All material appearing in the *Journal of Fish and Wildlife Management* is in the public domain and may be reproduced or copied without permission unless specifically noted with the copyright symbol ©. Citation of the source, as given above, is requested.

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

* Corresponding author: barbara_ann_martin@usgs.gov

Introduction

Accuracy and precision of age data is an important aspect to the management of fishes. Inaccurate age determination can lead to erroneous calculations for survival and growth and lead to false indications of recruitment failure or success. In their reviews, Beamish and McFarlane (1983) and Campana (2001) indicated the mismanagement of many commercial species due to the underestimation of ages that led to incorrect life history assumptions and poor estimations of survival and growth that in turn led to overfishing of these species.

However, when extremely rare species are incorrectly aged, management decisions that rely on age-based survival estimates could lead to false indications of recruitment failure or success, which in turn could lead to extinction.

Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers are jointly listed as endangered pursuant to the U.S. Endangered Species Act (ESA 1973, as amended; USFWS 1988). The U.S. Fish and Wildlife Service listed both species as endangered because of range contractions, declines in abundance, and a lack of evidence of recent recruitment to adult



populations (USFWS 1988). Upper Klamath Lake contains the largest remaining population of Lost River Suckers (National Research Council 2004) and one of the largest remaining populations of Shortnose Suckers (USFWS 2013). Clear Lake Reservoir also supports both species. Although a large population of suckers, classified as Shortnose Suckers, exists in Clear Lake Reservoir, this population appears morphologically different from the Upper Klamath Lake Shortnose Sucker population (Koch and Contreras 1973; Andreasen 1975; Miller and Smith 1981; Buettner and Scoppettone 1991), and, to date, genetic analysis has not separated the Clear Lake Reservoir Shortnose Suckers from Klamath Largescale Suckers, *Catostomus snyderi* (Smith et al. 2020).

In Upper Klamath Lake, recruitment of both species appears to be limited due to mortality of suckers during the juvenile life stage (National Research Council 2004; USFWS 2013). Although larval and age 0 suckers have been detected in large numbers during some years in Upper Klamath Lake, these cohorts do not appear to persist past age 2 (Burdick and Martin 2017). Sexual maturity occurs anywhere from age 4 to age 9 for Lost River Suckers and from age 4 to age 6 for Shortnose Suckers (USFWS 2013). However, monitoring of adult populations has not detected substantial recruitment of 4- to 7-y-old fish into spawning populations in nearly two decades (Hewitt et al. 2018). Size composition and capture–recapture results indicate that the abundance of both species in Upper Klamath Lake has decreased since the early 2000s and that the majority of suckers left in the spawning population is reaching senescence (Hewitt et al. 2018).

In Clear Lake Reservoir, length frequency data indicate intermittent recruitment of suckers to adult spawning populations (Hewitt and Hayes 2013; Hewitt et al. 2021). Recruitment failure in these populations appears to occur due to processes occurring at two points in the life history. A lack of small fish in some years indicates a failure of adults to spawn or a lack of survival from the egg to the juvenile life stage, whereas an abrupt decline in abundance when fish reach approximately 350 to 400 mm in fork length indicates high mortality around the time of the first spawning attempt. Accurate and precise aging data would allow us to assign poor survival and recruitment events to specific years. In turn, we could assess the effects of annual lake management on recruitment and survival.

Accurate aging of juvenile suckers is paramount to the recovery of these species. Managers require accurate juvenile sucker mortality estimates to assess, rank, and address the hypothesized causes of mortality. These causes include poor summertime water quality, parasites, bird predation, and a lack of suitable prey available from wetlands (Martin and Saiki 1999; Burdick 2013; Burdick et al. 2015; Evans et al. 2016; Janik et al. 2018). Because juvenile suckers are rare, elusive, and small in the first year of life, mortality estimation depends on catch-at-age methods rather than mark–recapture techniques. Catch-at-age estimation is dependent on accurate and precise age estimation. Overestimation of age may result in upward bias in survival estimates. Likewise, the under-

estimation of ages may bias survival estimates low. In addition, inaccurate aging used to describe the importance and diversity of life history strategies may place false importance on specific habitat types for restoration.

Previous studies used operculum and otoliths to age Lost River and Shortnose suckers (Scoppettone 1988; Buettner and Scoppettone 1991; Hoff et al. 1997; Terwilliger et al. 2010). Because removal of operculum or otoliths is lethal, recent studies (Burdick et al. 2016; Burdick et al. 2018; Bart et al. 2020a, 2020b; Bart et al. 2021) aged these fish using fin rays that can be removed nonlethally. To verify that more than one structure can be used to accurately age a fish, studies compared increment formation among structures (Sylvester and Berry 2006; Radford et al. 2021). No published studies that we are aware of compare aging of fin rays, opercula, and lapillus otoliths from Lost River or Shortnose suckers. Fin rays, opercles, and otolith sections display banding patterns that serve as records of relatively faster and slower growth periods. Slow growth is generally associated with environmental conditions such as cooler temperatures or lack of prey, creating a translucent increment in fin rays under transmitted light. Fast growth in fin rays is associated with an opaque region under transmitted light that spans a greater distance in young fish. Adverse environmental conditions that cause stress to the fish can disrupt this pattern in one or more of the structures, leading to false annuli and potential disagreement in aging among structures. Although useful in determining if different structures can be used to age a species, confirming similar increment formation among structures is not validation of annual increment formation.

Examining structures on fish captured repeatedly over time provides the most direct method for determining periodicity of increment formation (Beamish and McFarlane 1983; Isely and Grabowski 2007). However, this method does not provide information on the timing within each annual cycle that increments are formed. Marginal increment analysis is used to determine the timing of increment formation (Campana 2001). This method requires monthly samples to compare the distance from the last translucent increment to the edge of the structure (marginal increment) to determine the seasonal timing of increment formation (Campana 2001). Recently formed translucent increments are indicated by small distances, and the period of growth is indicated by large distances (Isely and Grabowski 2007). When plotted as a function of time, marginal increments should represent a sinusoidal cycle with a frequency of 1 y if a single annulus is present per year (Campana 2001). The lowest part of the sinusoidal cycle indicates the timing of a newly formed annulus.

The timing and periodicity of increment formation varies depending on the life stage of fish and environmental conditions. Terwilliger et al. (2010) determined that adult Lost River and Shortnose suckers deposit increments on lapillus otoliths annually in winter or early spring, but they lacked the sample size to adequately assess timing of increment formation in juvenile suckers. The act of reproduction often delays the timing of

increment formation in adult fish, which corresponds to a delay in the start of growth (Quinn and Ross 1982; Smith 2014). Therefore, it is important to validate the timing and annual periodicity of increment formation on fin rays of juvenile Lost River and Shortnose suckers under environmental conditions similar to those normally experienced by these suckers.

Upper Klamath Lake and Clear Lake Reservoir experience warm summers and cold winters, completely freezing over in most years. Upper Klamath Lake is hypereutrophic and experiences massive algal blooms in summer that are dominated by a single cyanobacterium, *Aphanizomenon flos-aquae*, that can lead to episodes of hypoxia/anoxia (Lindenberg et al. 2009), while Clear Lake Reservoir is turbid with no large algal blooms (Burdick et al. 2015). Spawning for both species occurs in the spring after ice-out, with the majority of activity in March and April. Given the annual cycle of temperature, summer fast-growth periods and winter slow-growth periods should be obvious in our specimens, at least during early years of life when substantial growth occurs. Poor water quality in Upper Klamath Lake may lead to the formation of false annuli.

We sought to validate the assumption that translucent increments on fin rays of juvenile endangered Lost River and Shortnose suckers are formed annually. To accomplish this goal, we examined fin rays from passive integrated transponder (PIT)-tagged suckers that we captured repeatedly over time in the semiclosed system of Hagelstein Pond, which is connected to Upper Klamath Lake, and conducted marginal increment analysis on the fin rays. We performed this study to improve confidence in the accuracy of age estimates of juvenile Lost River and Shortnose suckers using fin rays. Accurate age estimates are essential to increase confidence in the assessment of year-class formation, annual juvenile sucker survival indices, and information on early life histories of juvenile suckers, which researchers use to help guide the management of these species.

Methods

Fish sampling

We collected suckers used in this analysis from Hagelstein Pond located at the base of Modoc Rim adjacent to Upper Klamath Lake (Figure 1). In 1963, construction of Hagelstein Park separated a historic spawning area known as Barkley Springs from Upper Klamath Lake. In 2010, a restoration project reestablished connectivity of Hagelstein Pond to Upper Klamath Lake through the restoration of a meandering stream channel approximately 0.1 m deep, 0.7 m across, and 285 m long. Hagelstein Pond is fed by a spring that provides a fairly consistent temperature of 15–16°C. In 2014, biologists detected juvenile suckers of various sizes and presumably various ages in this historic spawning area of Lost River Suckers. Researchers routinely PIT tag suckers in Hagelstein Pond for another study, and they detected very few of the PIT-tagged suckers leaving the pond via the two stationary antennas located in the stream

channel at the exit. This semiclosed system provided the opportunity to observe suckers exposed to the same rearing conditions and to recapture some of these individuals over time. We assume Hagelstein Pond suckers are representative of the broader population of suckers in Upper Klamath Lake because Hagelstein suckers most likely emigrated from Upper Klamath Lake. However, rearing conditions in Hagelstein Pond appear to be better suited to the survival of juvenile suckers, as seen by the various size classes of suckers found in Hagelstein Pond compared with Upper Klamath Lake.

We captured fish using trap nets with mouth dimensions of 0.61 × 0.91 m, with a 15-m lead, three internal fykes, and 0.635-cm² delta knotless mesh. We deployed trap nets opportunistically from 2014 to 2016 and deployed five trap nets at fixed sampling sites during sampling events that occurred at least seasonally from 2017 to 2021. We did not identify suckers to species because juvenile Lost River and Shortnose suckers are morphologically indistinguishable, and we lacked sufficient genetic data to determine the complete species composition of our sample set. We measured standard length of captured suckers to the nearest millimeter. At first capture, we removed the leading left pectoral fin ray at the proximal joint for aging, and if the sucker was greater than 70 mm standard length, we inserted a PIT tag into the sucker. To avoid collection of regenerated fin rays, we removed the leading right pectoral fin for aging from recaptured suckers identified based on the presence of a PIT tag. For suckers recaptured a second time, we removed the secondary fin ray from their left pectoral fin.

Estimating age by enumerating translucent increments on fin rays

We dried fin rays, mounted them in epoxy, sectioned (0.6-mm thickness) them using a Buehler IsoMet low-speed precision saw (Uzwil, Switzerland), and viewed them under magnification (two experienced readers; Zeiss AxioStar microscope, Oberkochen, Germany) using transmitted light (Quist et al. 2012). We determined the number of translucent increments in blind reads, and each reader had no knowledge of the other's increment count. When both readers agreed on the number of increments, we presumed the estimated age was correct, and it was used in the analysis (Martin et al. 2022; Data S1, *Supplemental Material*). A third reader acted as a tie breaker when the first two readers disagreed on the estimated age based on the increment count. If all three readers disagreed on the age during the blind reads, the three readers examined the individual fin rays at the same time to reach a consensus age. We reported a proportion of exact agreement and agreement within one of the estimated ages for the fin rays read by the first two readers. As a first step in determining if the number of translucent increments could reasonably be interpreted as being laid down annually, we plotted the

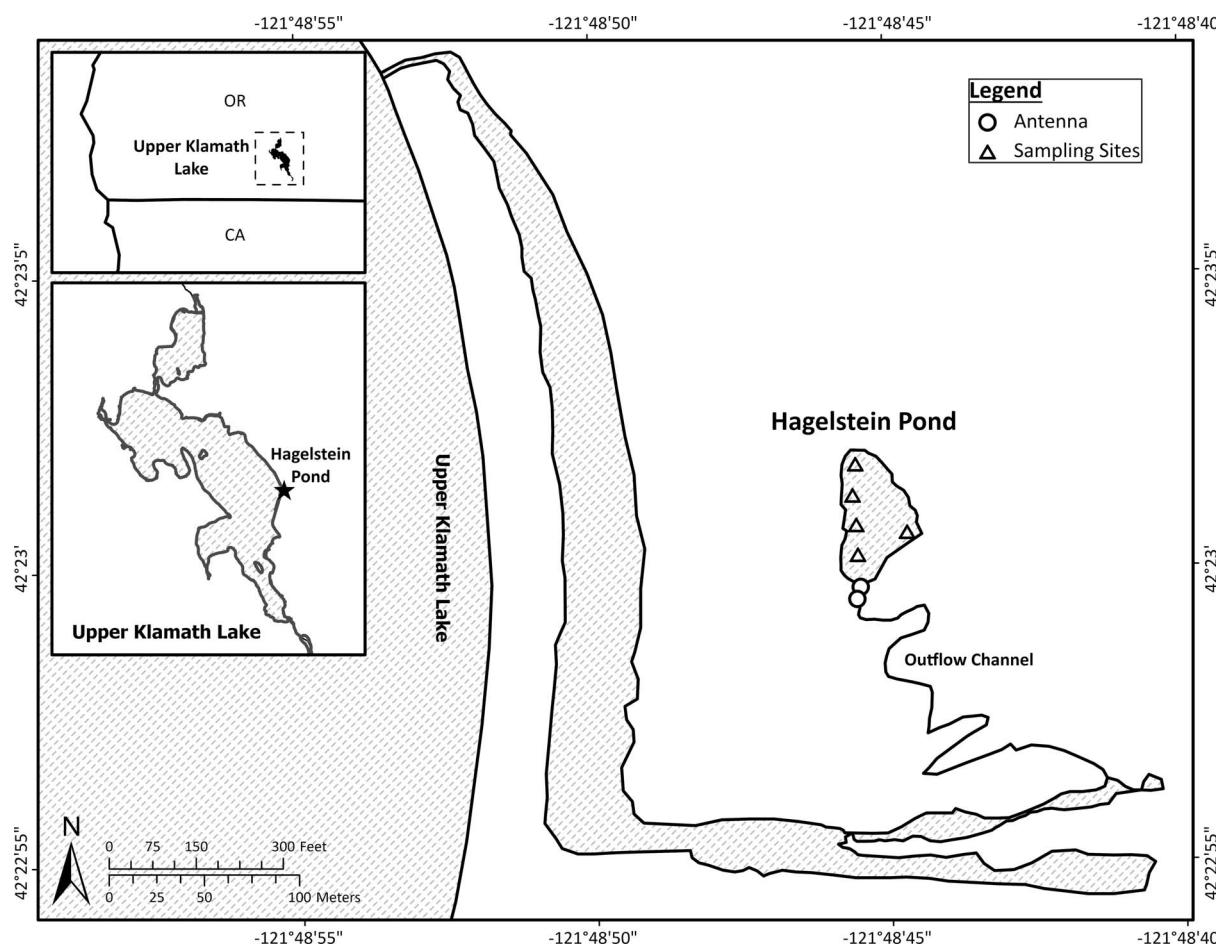


Figure 1. Map of Hagelstein Pond located adjacent to Upper Klamath Lake in Southern Oregon, USA. Fixed sampling locations (triangles) and placement of the antennas (circles) at the outflow channel of Hagelstein Pond are shown. Lost River *Deltistes luxatus* and Shortnose suckers *Chasmistes brevirostris* were collected from the sampling locations from 2014 through 2021 for age analysis.

estimated age by standard length to ensure that there were no obvious outliers.

Validation of annual increment formation using mark-recapture

To determine if translucent increments were deposited annually, we examined fin rays of fish captured on multiple occasions. We compared the number of years fish were at large between captures with the difference in increments at each capture. To determine if increments were deposited annually, we also considered time of year when each sample was collected and the likelihood of an annuli being laid down at that time of year (Martin et al 2022; Data S2, *Supplemental Material*). It was important that we compare the season of capture in addition to the year of capture, otherwise the number of translucent increments might appear to differ by 1 y from time at large.

Increment measurements

We photographed fin rays using an LW Scientific MiniVID USB microscope camera (Lawrenceville, GA) and

took measurements using TouView microimage analysis software (Touptek Photonics, Hangzhou, China). We did not measure fin rays that were cut at an angle because they did not have a similar shape to the remaining fin rays, and therefore we could not compare measurements. We took three measurements on each fin ray: 1) we took R from the core to the edge of the section, 2) we took R_n from the core to the first translucent increment from the outer edge and did not include the light-colored translucent increment, and 3) we took R_{n-1} from the core to the inside of the second from the edge translucent increment and did not include the width of the light-colored translucent increment (Figure 2). All measurements are available in Martin et al. (2022) and Data S1.

Analysis of increment periodicity

We used three complementary methods to determine the timing of translucent increment formation in juvenile suckers. For fish estimated to be age 1 or greater, we conducted an edge analysis in which we determined if a fin ray had a translucent or opaque edge (Buckmeier et

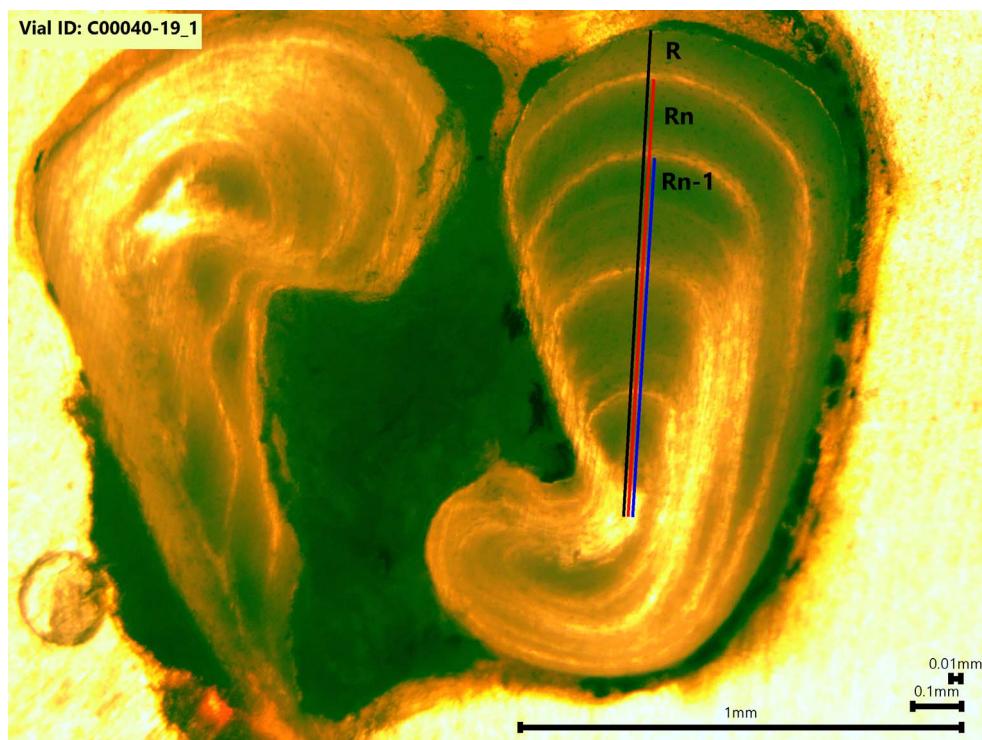


Figure 2. Example of fin ray section with radial measurements. R (black line) extended from the core to the edge of the section. R_n (red line) extended from the core to the first translucent increment. R_{n-1} (blue line) extended from the core to the second from the edge translucent increment. The fin ray was collected in 2019 from a juvenile sucker in Hagelstein Pond, Oregon. Photograph by Rachael Paul-Wilson, U.S. Geological Survey, September 1, 2022.

al. 2017). A translucent edge indicated a period of slow growth, while an opaque edge indicated that the sucker was in the midst of the growing season. We omitted samples cut at an angle due to the difficulty in determining a true translucent edge of fin rays cut at an angle. We plotted the monthly mean and standard error of both marginal increment measurements and marginal increment ratios. We measured marginal increment (MI), the distance between the start of the formation of the last translucent increment and the edge ($MI = R - R_n$; Buckmeier et al. 2017), for suckers estimated to be age 1 or greater. The marginal increment ratio (MIR) is the ratio of marginal increment to the increment width of the combination of translucent and opaque increments formed in the previous year ($MIR = MI/[R_n - R_{n-1}]$) (Buckmeier et al. 2017). The marginal increment ratio standardizes increment measurements across ages by determining a proportional state of completion in the last year compared with the prior year and therefore can only be calculated for fish at least 2 y of age.

On an individual-fish level, the width of the marginal increment or marginal increment ratio increases with time from formation of a translucent increment (Isely and Grabowski 2007). The mean of each of these measurements peaks just before some fish start forming a translucent increment, and a decline in mean marginal increment and marginal increment ratio indicates an increase in the proportion of fish forming a new translucent increment. A minimum plateau in marginal

increment and marginal increment ratio indicates the time period in which most fish form translucent increments (Isely and Grabowski 2007). Because variation in the timing of translucent increment formation is minimal within life stages, we combine samples across ages for our analysis as discussed above (Murie and Parkyn 2005; Strickland and Middaugh 2015).

Results

We aged suckers captured from Hagelstein Pond as 0–7 y (Table 1). We identified age 0 fish by the time of year captured (fall) coupled with the size of the fish at capture and the lack of a translucent increment. We captured suckers presumed to be age 0 in half the years of our study, while we captured fish estimated to be age 1 in most years. We could identify year-classes through time until they reached either age 6 or age 7 (Table 1). Fish lengths generally increased with estimated age, and growth appeared to slow around age 3 or age 4 (Figure 3).

The first two fin ray readers agreed exactly on the number of translucent increments 70% of the time and were within ± 1 putative annuli 98% of the time (Figure 4). The first two readers agreed 79% of the time for fish estimated to be age 3 or less (99% within one increment) and 62% of the time for fish estimated to be greater than age 3 (97% within one increment). We did not detect reader bias in translucent increment enumeration. Most

Table 1. The combined numbers of Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers that we captured from Hagelstein Pond, Oregon, per year (2014–2021) by estimated age. We estimated ages based on the number of translucent increments counted on fin rays. The numbers of suckers measured for marginal increment analysis are in parentheses.

Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
2014	10 (0)	5 (5)	2 (2)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
2015	4 (0)	17 (12)	6 (5)	5 (4)	3 (1)	0 (0)	0 (0)	0 (0)
2016	0 (0)	1 (1)	4 (4)	5 (4)	1 (1)	0 (0)	0 (0)	0 (0)
2017	0 (0)	6 (2)	44 (40)	33 (32)	9 (8)	3 (3)	1 (1)	0 (0)
2018	0 (0)	0 (0)	9 (6)	25 (22)	13 (11)	1 (1)	1 (1)	0 (0)
2019	1 (0)	1 (1)	0 (0)	3 (1)	31 (24)	15 (14)	3 (3)	1 (1)
2020	0 (0)	1 (1)	2 (2)	0 (0)	16 (12)	34 (31)	11 (8)	2 (2)
2021	2 (0)	0 (0)	5 (5)	2 (2)	1 (1)	10 (9)	45 (40)	14 (11)

disagreements in estimated age were associated with determination of the presence of a translucent increment on the edge. The third fin ray reader agreed with one of the first two readers 89% of the time. All three readers examined the remaining 14 fin rays together to determine an age by consensus.

We captured 58 suckers on multiple occasions (Table 2). The time span between recapturing fish occurred anywhere from the same year to 7 y later. We observed elapsed estimated ages in all recaptured individuals that matched expected values based on time elapsed and the time of year of first and second captures. This included the suckers that we initially captured without translucent increments (presumed age 0), indicating that the first translucent increment was laid down at age 1. We recaptured 6 of the 58 individuals on a third occasion either the same year ($N = 4$) or 1 y after ($N = 2$) the previous capture. One fish was from the 2013 year-class,

two fish were from the 2014 year-class, and three fish were from the 2015 year-class.

Sample sizes were insufficient for age- or year-specific analysis with the possible exception of 2017 (Table 1). Although we collected close to 100 samples in 2017, we did not collect fish during five of the months (Table 3). Consequently, we pooled samples by month across ages and years in our analysis for edge analysis, marginal increment analysis, and marginal increment ratios.

The edge analysis on fish estimated to be age 1 or older ($N = 335$) indicated a sinusoidal cycle in increment formation with a frequency of 1 y. The portion of fin rays with a translucent edge increased most between December and February and decreased most between February and July (Figure 5). February had the greatest proportion of fin rays with a translucent edge. More than 50% of the fin rays that we examined during each month January to April had a translucent edge, whereas fewer

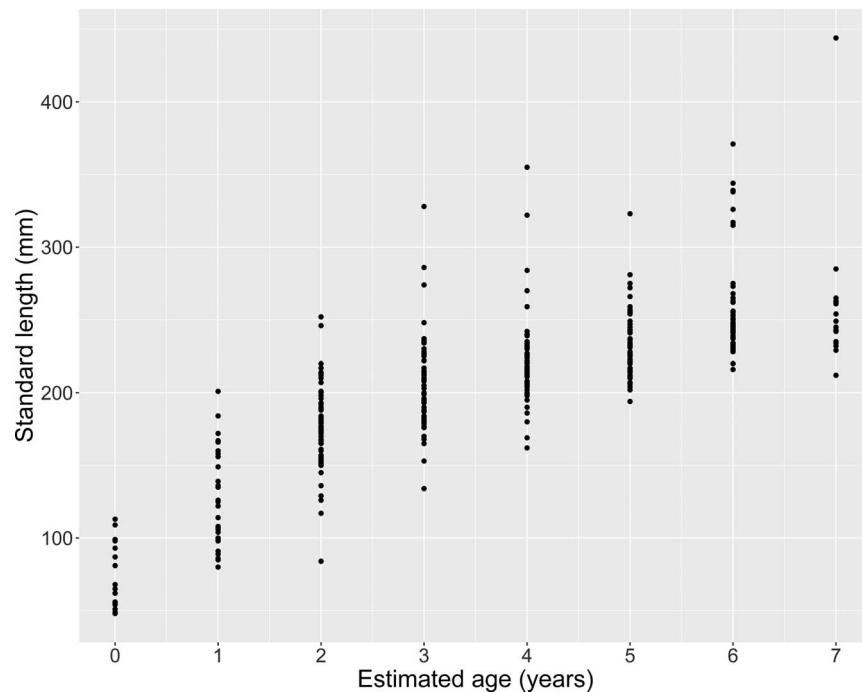


Figure 3. Relationship between estimated age and standard length of the combination of juvenile Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers captured from Hagelstein Pond, Oregon, from 2014 to 2021. We estimated ages based on the number of translucent increments counted on fin rays.

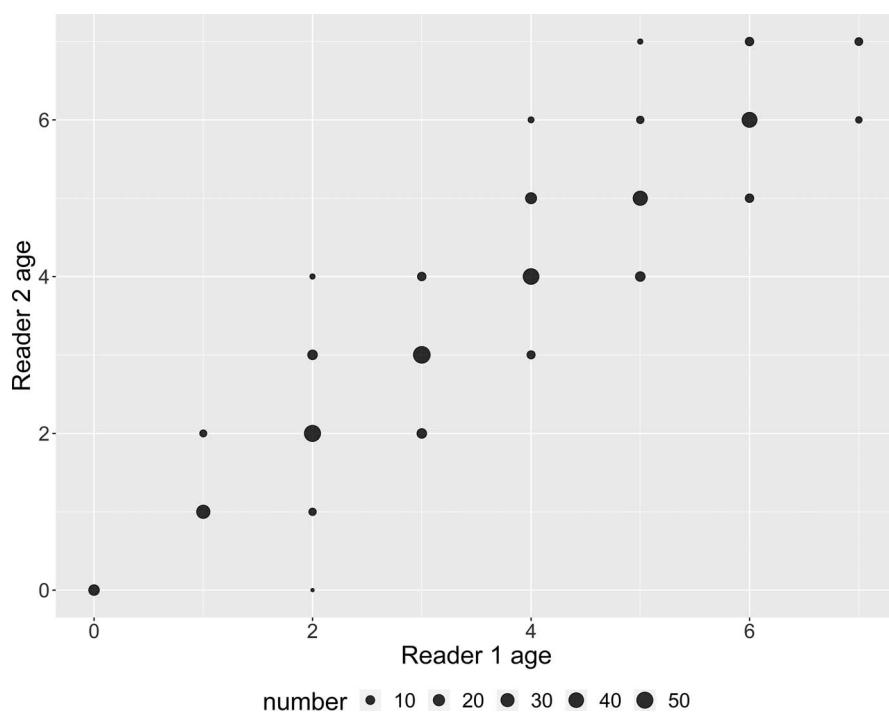


Figure 4. Comparison of fin ray ages determined by two individuals (reader 1 and reader 2) of the combination of Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers collected from Hagelstein Pond, Oregon, from 2014 to 2021. The size of the circle is related to the number of specimens given in each combination.

Table 2. The combined number of Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers recaptured in Hagelstein Pond, Oregon, from 2014 to 2021 based on initial estimated age of capture and estimated age of first recapture. We estimated ages based on the number of translucent increments counted on fin rays. Dashes represent combinations that are not possible.

Initial age of capture	Age of recapture							
	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
Age 0	0	0	0	0	1	0	1	1
Age 1	—	0	0	3	3	3	0	0
Age 2	—	—	2	2	2	1	14	0
Age 3	—	—	—	3	3	0	2	2
Age 4	—	—	—	—	3	0	4	1
Age 5	—	—	—	—	—	1	2	2
Age 6	—	—	—	—	—	—	0	1
Age 7	—	—	—	—	—	—	—	1

Table 3. Number of fin rays that we collected from the combination of Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers from Hagelstein Pond, Oregon, by month and year (2014–2021) measured for edge analysis and marginal increment followed by number of fish in parentheses that we measured for marginal increment ratio.

Month	2014	2015	2016	2017	2018	2019	2020	2021
January	0 (0)	0 (0)	0 (0)	0 (0)	7 (7)	0 (0)	3 (3)	11 (11)
February	0 (0)	0 (0)	0 (0)	0 (0)	4 (4)	5 (5)	0 (0)	1 (1)
March	0 (0)	0 (0)	0 (0)	0 (0)	4 (4)	0 (0)	7 (7)	3 (3)
April	0 (0)	0 (0)	0 (0)	3 (3)	0 (0)	7 (7)	0 (0)	6 (6)
May	0 (0)	0 (0)	10 (9)	7 (7)	0 (0)	0 (0)	9 (9)	10 (10)
June	0 (0)	0 (0)	0 (0)	8 (8)	0 (0)	0 (0)	30 (29)	27 (27)
July	0 (0)	10 (3)	0 (0)	0 (0)	12 (12)	6 (6)	2 (2)	2 (2)
August	2 (0)	0 (0)	0 (0)	4 (4)	8 (8)	13 (13)	5 (5)	0 (0)
September	6 (3)	12 (7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (2)
October	0 (0)	0 (0)	0 (0)	36 (34)	0 (0)	0 (0)	0 (0)	1 (1)
November	0 (0)	0 (0)	0 (0)	24 (24)	2 (2)	8 (8)	0 (0)	0 (0)
December	0 (0)	0 (0)	0 (0)	4 (4)	4 (4)	5 (4)	0 (0)	5 (5)
Total	8 (3)	22 (10)	10 (9)	86 (84)	41 (41)	44 (43)	56 (55)	68 (68)

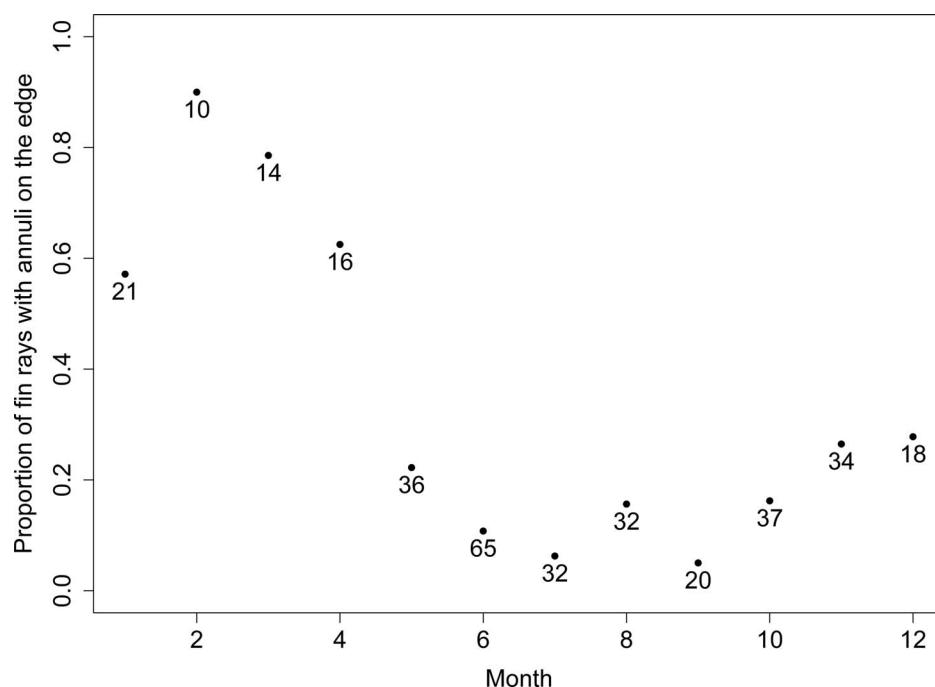


Figure 5. Proportion of fin rays that we collected from the combination of Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers that had a translucent outer edge by month of collection. The sample size is noted under each sample point. We collected suckers from Hagelstein Pond, Oregon, from 2014 to 2021.

than 20% of fin rays had translucent edges between June and October.

We completed the marginal increment analysis on 335 fish that we estimated to be age 1 or greater, and we completed marginal increment analysis ratio calculations on 313 fish that we estimated to be age 2 or greater. Both measurements had a minimum plateau from February to April (Figure 6). Marginal increment and marginal increment ratio increased beginning around June or July and peaked in September. Marginal increment began to decrease between September and October, and marginal increment ratio began to decrease between November and December. Both measurements exhibited a gradual decline from September to February, although the pattern was clearer from marginal increment than from marginal increment ratio data. Both marginal increment and marginal increment ratio indicated that increment formation occurred with a frequency of 1 y.

Discussion

This study provides the first validation of a nonlethal aging method for the endangered Lost River and Shortnose suckers using translucent increment formation in fin rays and the first validation of increment formation on any structure type for these juvenile suckers. While we did not validate age estimation against known aged fish, as recommended by Beamish and McFarlane (1983) and Campana (2001), fin rays examined over time on tagged fish show that juvenile suckers formed translucent increments annually. Furthermore, the recapture of several suckers that we initially captured as age 0 in the

fall validated that the first increment was laid down at age 1. Our marginal increment analysis confirmed annual increment formation for juvenile Lost River and Shortnose suckers. This analysis also provided additional information on the annual timing of increment formation, which is important to interpreting fin ray increments as age estimates.

The three methods we used indicated that translucent increments for juvenile Lost River and Shortnose suckers formed from October to May and peaked in late winter and early spring. A decrease in marginal increment beginning around October indicated that translucent increments began to form in the fall. Small marginal increments from February to April and somewhat from January to May indicated that translucent increment formation on juvenile sucker fin rays was most frequent from winter to spring. Our marginal increment ratio analysis corroborated this result with less precision and generally indicated that translucent increment formation started around December and peaked from February to April. Edge analysis indicated the window of frequent translucent increment formation may also include January and that increment formation peaked in February. The timing of the formation of translucent increments corresponds to decreased growth, which is linked to decreased water temperatures. Water temperature in Upper Klamath Lake generally declines below 15°C in October and increases above 15°C in May, with temperatures approaching 25°C in July and August (Morace 2007).

In a study of adult Lost River and Shortnose suckers, Terwilliger et al. (2010) reported a decrease in marginal increment ratio on lapillus otoliths between November

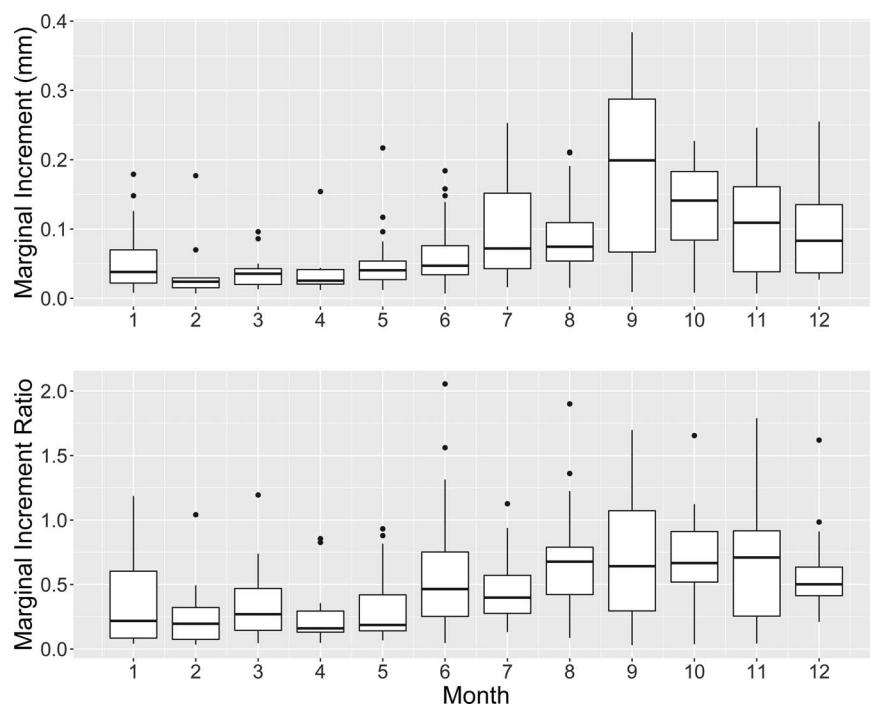


Figure 6. Box plot (box represents the median and the 25 and 75% quartiles, with whiskers showing the minimum and maximum values and outliers represented by dots) of marginal increments and marginal increment ratios by months. We took measurements from fin rays that we collected from Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers captured in Hagelstein Pond, Oregon, from 2014 to 2021.

and February. However, they had no samples from December or January, and they collected only eight total samples in February and March, of which one had a marginal increment ratio around 0.7. Therefore, Terwilliger et al. (2010) were unable to determine when increment formation started or peaked, only that it appeared to be complete by April. These two data sets corroborate each other, indicating that Lost River and Shortnose suckers form translucent increments annually beginning in the fall. Our data set provides additional resolution on the timing of increment formation on fin rays of juvenile suckers by indicating the timing of peak formation.

A common difficulty in edge and marginal increment analysis is determining the presence of slow growth increments near the edge of a fin ray or otolith (Campana 2001). A lack of agreement about the presence of a terminal translucent increment affected among-reader precision in age estimation in our study. Falsely identifying the presence or absence of a final translucent increment may have contributed to the imprecision in mean monthly marginal increment widths and our conclusions about the timing of translucent increment formation. Our marginal increment analysis determined the timing of translucent increment formation, which can be used in the future to disregard edge increments for juvenile suckers when they are collected during periods when increments should not be forming on the edge. However, this approach may not be appropriate for older suckers that do not have discern-

able growth bands and therefore are more difficult to age.

The timing of annual increment formation on fin rays or otoliths can vary among species primarily due to differences in habitat use and diet (Quinn and Ross 1982; Lessa et al. 2006; Simmons and Beckman 2012; Smith 2014). Lost River and Shortnose suckers have similar life history traits, occupy similar habitats, and appear to have similar diets as juveniles (Markle and Clauson 2006). Due to these similarities, it is expected that the timing and periodicity of increment formation will be similar for the two species. In our study, we pooled samples over sucker species because of the difficulty in obtaining large sample sizes of these rare species and a lack of genetic data needed to distinguish these species. Species-specific differences are unlikely to be a major contributor to the variation in translucent increment formation in our study. However, due to variation in environmental conditions and species-specific differences, our results cannot automatically be applied to other species.

Life stage also can contribute to differences in timing of annual increment formation on fin rays or otoliths (Quinn and Ross 1982; Lessa et al. 2006; Simmons and Beckman 2012; Smith 2014). While we combined samples across ages, as recommended by Murie and Parkyn (2005) and Strickland and Middaugh (2015), we did not combine samples across life stages. Reproduction, which often delays the start of growth and therefore the deposition of a translucent increment (Quinn and Ross 1982; Smith 2014), was not a factor in altering timing of increment formation for juvenile suckers examined in our

study. Therefore, pooling across ages was likely not a major factor in the variation in timing of increment formation in our samples.

Conducting marginal increment analysis on a single cohort collected in a single year is ideal for reducing variation in estimates of the timing of increment formation (Campana 2001). Due to the rarity of juvenile Lost River and Shortnose suckers, we pooled suckers across years to produce large enough sample sizes for our analysis. Increment formation often occurs during the winter months when growth slows due to a slower metabolism and decreased food resources (Fey 2005; Gumus et al. 2007; Beckman and Calfee 2014), but cool temperatures are the primary factor driving increment formation (Fey 2005). Timing of growth depends on annual weather patterns, and the timing of increment formation can vary slightly from year to year (Lessa et al. 2006). Therefore, pooling samples across years was likely to be a major factor affecting the monthly variation in marginal increment measurements in our analysis.

Translucent increments form on fin rays of juvenile suckers concurrent with cold water temperatures. This is consistent with the description of increment formation on hard structures of fish in temperate climates (Quist et al. 2012). Our marginal increment analyses indicated that translucent increment formation occurred from October to April and peaked from February to April in juvenile suckers. The peak in timing of translucent increment formation corresponded with the icing over of Upper Klamath Lake.

Increment formation timing is likely to be similar among Hagelstein Pond, Upper Klamath Lake, and Clear Lake Reservoir due to similar climates among these locations. In all three water bodies, water temperature varies with air temperature (USGS 2022). Due to spring influence, the variation in seasonal water temperature is lower in Hagelstein Pond than in Upper Klamath Lake or Clear Lake Reservoir. The greater variability in water temperatures in the lakes may cause annuli to be more pronounced in these habitats than in Hagelstein Pond, but the timing of formation would be similar.

Here, we provided the necessary validation of a nonlethal aging method by using fin rays to accurately estimate ages of juvenile Lost River and Shortnose suckers. Although it is essential to validate aging techniques for each species and structure, our study indicates that it is likely that fin rays can also be used to accurately age juveniles of other long-lived suckers. Accurate aging of fish is important for managing populations.

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. Data file containing information associated with each fin ray that we collected from Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris*

suckers from Hagelstein Pond, Oregon, 2014–2021. Associated data included with each fin ray (vial-ID) include date of capture, age determined by three independent researchers (read 1–3), final age, standard length (SL) of fish, radius of fin ray (R:L1), radius from core to last completed annuli of fin ray (Rn:L2), radius from the core to the second to last completed annuli of the fin ray (Rn-1:L3), determination of whether an annuli is on the edge of the fin ray, measurement from the last completed annuli to the edge of the fin ray (MI), measurement between the last two completed annuli (L2-L3), and ratio of MI to L2-L3.

Available: <https://doi.org/10.3996/JFWM-22-039.S1> (27 KB XLSX)

Data S2. Data file containing age and length data from individual Lost River *Deltistes luxatus* and Shortnose *Chasmistes brevirostris* suckers that we captured on multiple occasions from Hagelstein Pond, Oregon, 2014–2021. We identified individual suckers via a unique passive integrated transponder tag inserted into each sucker. Associated data for each individual fish include date of capture (date 1–3), standard length at date of capture (SL 1–3), vial identification for collected fin rays (vial 1–3), and age at capture (age 1–3).

Available: <https://doi.org/10.3996/JFWM-22-039.S2> (5 KB XLSX)

Reference S1. Bart RJ, Burdick SM, Hoy MS, Ostberg CO. 2020a. Juvenile Lost River and Shortnose sucker year-class formation, survival, and growth in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California—2017 monitoring report. Reston, Virginia: U.S. Geological Survey Open-File Report 2020-1025.

Available: <https://doi.org/10.3996/JFWM-22-039.S3> (1.673 MB PDF) and <https://pubs.er.usgs.gov/publication/ofr20201025>

Reference S2. Bart RJ, Burdick SM, Hoy MS, Ostberg CO. 2020b. Juvenile Lost River and Shortnose sucker year-class formation, survival, and growth in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California—2018 monitoring report. Reston, Virginia: U.S. Geological Survey Open-File Report 2020-1064.

Available: <https://doi.org/10.3996/JFWM-22-039.S4> (1.855 MB PDF) and <https://pubs.er.usgs.gov/publication/ofr20201064>

Reference S3. Bart RJ, Kelsey CM, Burdick SM, Hoy MS, Ostberg CO. 2021. Growth, survival, and cohort formation of juvenile Lost River (*Deltistes luxatus*) and Shortnose suckers (*Chasmistes brevirostris*) in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California—2019 monitoring report. Reston, Virginia: U.S. Geological Survey Open-File Report 2021-1119.

Available: <https://doi.org/10.3996/JFWM-22-039.S5> (3.271 MB PDF) and <https://doi.org/10.3133/ofr20211119>

Reference S4. Buettner ME, Scoppettone GG. 1991. Distribution and information on the taxonomic status of the Shortnose sucker (*Chasmistes brevirostris*) and Lost

River suckers (*Deltistes luxatus*) in the Klamath River Basin, California. Reno, Nevada: Seattle National Fishery Research Center.

Available: <https://doi.org/10.3996/JFWM-22-039.S6> (22.101 MB PDF)

Reference S5. Burdick SM. 2013 Assessing movement and sources of mortality of juvenile catostomids using passive integrated transponder tags, Upper Klamath Lake, Oregon—summary of 2012 effort. Reston, Virginia: U.S. Geological Survey Open File Report 2013-1062.

Available: <https://doi.org/10.3996/JFWM-22-039.S7> (334 KB PDF) and <https://doi.org/10.3133/ofr20131062>

Reference S6. Burdick SM, Elliott DG, Ostberg CO, Conway CM, Dolan-Caret A, Hoy MS, Feltz KP, Echols KR. 2015. Health and condition of endangered juvenile Lost River and Shortnose suckers relative to water quality and fish assemblages in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California. Reston, Virginia: U.S. Geological Survey Open-File Report 2015-1217.

Available: <https://doi.org/10.3996/JFWM-22-039.S8> (1.030 MB PDF) and <https://doi.org/10.3133/ofr20151217>

Reference S7. Burdick SM, Martin BA. 2017. Interannual variability in apparent relative production, survival, and growth of juvenile Lost River and Shortnose suckers in Upper Klamath Lake, Oregon, 2001–15. Reston, Virginia: U.S. Geological Survey Open-File Report 2017-1069.

Available: <https://doi.org/10.3996/JFWM-22-039.S9> (3.760 MB PDF) and <https://doi.org/10.3133/ofr20171069>

Reference S8. Burdick SM, Ostberg CO, Hereford ME, Hoy MS. 2016. Juvenile sucker cohort tracking data summary and assessment of monitoring program, 2015. Reston, Virginia: U.S. Geological Survey Open-File Report 2016-1164.

Available: <https://doi.org/10.3996/JFWM-22-039.S10> (1.485 MB PDF) and <https://doi.org/10.3133/ofr20161164>

Reference S9. Burdick SM, Ostberg CO, Hoy MS. 2018. Juvenile Lost River and Shortnose sucker year class strength, survival, and growth in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California—2016 monitoring report. Reston, Virginia: U.S. Geological Survey Open-File Report 2018-1066.

Available: <https://doi.org/10.3996/JFWM-22-039.S11> (1.651 MB PDF) and <https://doi.org/10.3133/ofr20181066>

Reference S10. Hewitt DA, Hayes BS. 2013. Monitoring of adult Lost River and Shortnose suckers in Clear Lake Reservoir, California, 2008–2010. Reston, Virginia: U.S. Geological Survey Open-File Report 2013-1301.

Available: <https://doi.org/10.3996/JFWM-22-039.S12> (896 KB PDF) and <https://doi.org/10.3133/ofr20131301>

Reference S11. Hewitt DA, Hayes BS, Harris AC, Janney EC, Kelsey CM, Perry RW, Burdick SM. 2021. Dynamics of endangered sucker populations in Clear

Lake Reservoir, California. Reston Virginia: U.S. Geological Survey Open-File Report 2021-1043.

Available: <https://doi.org/10.3996/JFWM-22-039.S13> (12.123 MB PDF) and <https://doi.org/10.3133/ofr20211043>

Reference S12. Hewitt DA, Janney EC, Hayes BS, Harris AC. 2018. Status and trends of adult Lost River (*Deltistes luxatus*) and Shortnose (*Chasmistes brevirostris*) sucker populations in Upper Klamath Lake, Oregon, 2017. Reston, Virginia: U.S. Geological Survey Open-File Report 2018-1064.

Available: <https://doi.org/10.3996/JFWM-22-039.S14> (885 KB PDF) and <https://doi.org/10.3133/ofr20181064>

Reference S13. Lindenberg MK, Hoilman G, Wood TM. 2009. Water quality conditions in Upper Klamath and Agency Lakes, Oregon, 2006. Reston, Virginia: U.S. Geological Survey Scientific Investigations Report 2008-5201.

Available: <https://doi.org/10.3996/JFWM-22-039.S15> (3.128 MB PDF) and <https://doi.org/10.3133/sir20085201>

Reference S14. Morace JL. 2007. Relation between selected water-quality variables, climatic factors, and lake levels in Upper Klamath and Agency Lakes, Oregon, 1990–2006. Reston, Virginia: U.S. Geological Survey Scientific Investigations Report 2007-5117. Available: <https://doi.org/10.3996/JFWM-22-039.S16> (2.113 MB PDF) and <https://doi.org/10.3133/sir20075117>

Reference S15. Smith M, Von Bargen J, Smith C, Miller M, Rasmussen J, Hewitt DA. 2020. Characterization of the genetic structure of four sucker species in the Klamath River—final report. Longview, Washington: U.S. Fish and Wildlife Service, Abernathy Fish Technology Center.

Available: <https://doi.org/10.3996/JFWM-22-039.S17> (851 KB PDF) and <https://www.fws.gov/office/abernathy-fish-technology-center/library>

Reference S16. [USFWS] U.S. Fish and Wildlife Service. 2013. Revised recovery plan for the Lost River sucker (*Deltistes luxatus*) and Shortnose sucker (*Chasmistes brevirostris*). Sacramento, California: U.S. Fish and Wildlife Service, Pacific Southwest Region.

Available: <https://doi.org/10.3996/JFWM-22-039.S18> (2.131 MB PDF) and <https://ecos.fws.gov/ecp/species/5604>

Acknowledgments

We thank the field staff from the U.S. Geological Survey Klamath Falls Field Station from 2014 to 2021 for assistance with collecting and processing the juvenile field data. We also thank A. Harris and C. Kelsey from the U.S. Geological Survey for their assistance in database management and queries. We would like to thank L. Wetzel and M. Buettner for reviewing the early version of the manuscript. In addition, we would like to thank the

Associate Editor and the thoughtful reviews by two anonymous journal reviewers, which immensely improved the manuscript. This publication was funded by the Bureau of Reclamation (Reclamation) and U.S. Geological Survey, U.S. Department of Interior. Funding was provided by Reclamation as part of its mission to manage, develop, and protect water and related resources in an environmentally and economically sound manner in the interest of the American public. Funding was provided through Interagency Agreement R18PG00062. Original data were released by Martin et al. (2022) and are available at <https://doi.org/10.5066/P903M7XU>.

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.

References

- Andreasen JK. 1975. Systematics and status of the family Catostomidae in Southern Oregon. PhD thesis. Corvallis: Oregon State University.
- Bart RJ, Burdick SM, Hoy MS, Ostberg CO. 2020a. Juvenile Lost River and Shortnose sucker year-class formation, survival, and growth in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California—2017 monitoring report. Reston, Virginia: U.S. Geological Survey Open-File Report 2020-1025. Available: <https://pubs.er.usgs.gov/publication/ofr20201025> (April 2022; see Supplemental Material, Reference S1)
- Bart RJ, Burdick SM, Hoy MS, Ostberg CO. 2020b. Juvenile Lost River and Shortnose sucker year-class formation, survival, and growth in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California—2018 monitoring report. Reston, Virginia: U.S. Geological Survey Open-File Report 2020-1064. Available: <https://pubs.er.usgs.gov/publication/ofr20201064> (April 2022; see Supplemental Material, Reference S2)
- Bart RJ, Kelsey CM, Burdick SM, Hoy MS, Ostberg CO. 2021. Growth, survival, and cohort formation of juvenile Lost River (*Deltistes luxatus*) and Shortnose suckers (*Chasmistes brevirostris*) in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California—2019 monitoring report. Reston, Virginia: U.S. Geological Survey Open-File Report 2021-1119. Available: <https://pubs.er.usgs.gov/publication/ofr20211119> (April 2022; see Supplemental Material, Reference S3).
- Beamish RJ, McFarlane GA. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 131:735–743.
- Beckman DW, Calfee JW. 2014. Timing of first annulus formation in white sucker otoliths. North American Journal of Fisheries Management 34:1187–1189.
- 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.
- Buettner ME, Scoppettone GG. 1991. Distribution and information on the taxonomic status of the Shortnose sucker (*Chasmistes brevirostris*) and Lost River suckers (*Deltistes luxatus*) in the Klamath River Basin, California. Reno, Nevada: Seattle National Fishery Research Center (see Supplemental Material, Reference S4).
- Burdick SM. 2013 Assessing movement and sources of mortality of juvenile catostomids using passive integrated transponder tags, Upper Klamath Lake, Oregon—summary of 2012 effort. Reston, Virginia: U.S. Geological Survey Open File Report 2013-1062. Available: <https://doi.org/10.3133/ofr20131062> (see Supplemental Material, Reference S5).
- Burdick SM, Elliott DG, Ostberg CO, Conway CM, Dolan-Caret A, Hoy MS, Feltz KP, Echols KR. 2015. Health and condition of endangered juvenile Lost River and Shortnose suckers relative to water quality and fish assemblages in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California. Reston, Virginia: U.S. Geological Survey Open-File Report 2015-1217. Available: <https://doi.org/10.3133/ofr20151217> (see Supplemental Material, Reference S6).
- Burdick SM, Martin BA. 2017. Inter-annual variability in apparent relative production, survival, and growth of juvenile Lost River and Shortnose suckers in Upper Klamath Lake, Oregon, 2001–15. Reston, Virginia: U.S. Geological Survey Open-File Report 2017-1069. Available: <https://doi.org/10.3133/ofr20171069> (see Supplemental Material, Reference S7).
- Burdick SM, Ostberg CO, Hereford ME, Hoy MS. 2016. Juvenile sucker cohort tracking data summary and assessment of monitoring program, 2015. Reston, Virginia: U.S. Geological Survey Open-File Report 2016-1164. Available: <http://doi.org/10.3133/ofr20161164> (see Supplemental Material, Reference S8).
- Burdick SM, Ostberg CO, Hoy MS. 2018. Juvenile Lost River and Shortnose sucker year class strength, survival, and growth in Upper Klamath Lake, Oregon, and Clear Lake Reservoir, California—2016 monitoring report. Reston, Virginia: U.S. Geological Survey Open-File Report 2018-1066. Available: <https://doi.org/10.3133/ofr20181066> (see Supplemental Material, Reference S9).
- Campana SE. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197–242.
- Evans AG, Hewitt DA, Payton Q, Cramer BM, Collis K, Roby DD. 2016. Colonial water bird predation on Lost River and Shortnose suckers in the Upper Klamath Basin. North American Journal of Fisheries Management 36:1254–1268.
- Fey DP. 2005. Is the marginal otolith increment width a reliable recent growth index for larval and juvenile herring? Journal of Fish Biology 66:1692–1703.

- Gumus A, Bostanci D, Yilmaz S, Polat N. 2007. Age determination of *Scardinius erythrophthalmus* (Cyprinidae) inhabiting Bafra Fish Lakes (Samsun, Turkey) based on otolith readings and marginal increment analysis. *Cybium* 31:59–66.
- Hewitt DA, Hayes BS. 2013. Monitoring of adult Lost River and Shortnose suckers in Clear Lake Reservoir, California, 2008–2010. Reston, Virginia: U.S. Geological Survey Open-File Report 2013-1301. Available: <https://doi.org/10.3133/ofr20131301> (see *Supplemental Material*, Reference S10).
- Hewitt DA, Hayes BS, Harris AC, Janney EC, Kelsey CM, Perry RW, Burdick SM. 2021. Dynamics of endangered sucker populations in Clear Lake Reservoir, California. Reston, Virginia: U.S. Geological Survey Open-File Report 2021-1043. Available: <https://doi.org/10.3133/ofr20211043> (see *Supplemental Material*, Reference S11).
- Hewitt DA, Janney EC, Hayes BS, Harris AC. 2018. Status and trends of adult Lost River (*Deltistes luxatus*) and Shortnose (*Chasmistes brevirostris*) sucker populations in Upper Klamath Lake, Oregon, 2017. Reston, Virginia: U.S. Geological Survey Open-File Report 2018-1064. Available: <https://doi.org/10.3133/ofr20181064> (see *Supplemental Material*, Reference S12).
- Hoff GR, Logan DJ, and Markle DK. 1997. Otolith morphology and increment validation in young Lost River and Shortnose suckers. *Transactions of the American Fisheries Society* 126:488–494.
- Isely JJ, Grabowski TB. 2007. Age and growth. Pages 187–228 in Guy CS, Brown ML, editors. *Analysis and interpretation of freshwater fisheries data*. Bethesda, Maryland: American Fisheries Society.
- Janik AJ, Markle DF, Heidel JR, Kent ML. 2018. Histopathology and external examination of heavily parasitized Lost River Sucker *Deltistes luxatus* (Cope 1879) and Shortnose Sucker *Chasmistes brevirostris* (Cope 1879) from Upper Klamath Lake, Oregon. *Journal of Fish Diseases* 41:1675–1687.
- Koch DL, Contreras GP. 1973. Preliminary survey of the fishes of the Lost River system including Lower Klamath Lake and Klamath Strait Drain with special reference to the Shortnose (*Chasmistes brevirostris*) and Lost River (*Catostomus luxatus*) suckers. Reno, Nevada: Desert Research Institute, Center for Water Resources Research.
- Lessa R, Santana FM, Duarte-Neto P. 2006. A critical appraisal of marginal increment analysis for assessing temporal periodicity in band formation among tropical sharks. *Environmental Biology Fishes* 77:309–315.
- Lindenberg MK, Hoilman G, Wood TM. 2009. Water quality conditions in Upper Klamath and Agency Lakes, Oregon, 2006. Reston, Virginia: U.S. Geological Survey Scientific Investigations Report 2008-5201 (see *Supplemental Material*, Reference S13).
- Markle DF, Clauson K. 2006. Ontogenetic and habitat-related changes in diet of late larval and juvenile suckers (Catostomidae) in Upper Klamath Lake, Oregon. *Western North American Naturalist* 66:492–501.
- Martin BA, Burdick SM, Paul-Wilson RK, Bart RJ. 2022. Marginal increment and age data from fin rays of endangered suckers. Reston, Virginia: U.S. Geological Survey, Klamath Falls Field Station, Klamath Falls, Oregon. U.S. Geological Survey, data release. Available: <https://doi.org/10.5066/P903M7XU>
- Martin BA, Saiki MK. 1999. Effects of ambient water quality on the endangered Lost River sucker in Upper Klamath Lake, Oregon. *Transactions of the American Fisheries Society* 128:953–961.
- Miller RR, Smith GR. 1981. Distribution and evolution of *Chasmistes* (Pisces Catostomidae) in western North America. *Occasional Papers of the Museum of Zoology*, University of Michigan 696:1–46.
- Morace JL. 2007. Relation between selected water-quality variables, climatic factors, and lake levels in Upper Klamath and Agency Lakes, Oregon, 1990–2006. Reston, Virginia: U.S. Geological Survey Scientific Investigations Report 2007-5117 (see *Supplemental Material*, Reference S14).
- Murie DJ, Parkyn DC. 2005. Age and growth of white grunt (*Haemulon plumieri*): a comparison of two populations along the west coast of Florida. *Bulletin of Marine Science* 76:73–93.
- National Research Council. 2004. *Endangered and threatened fishes in the Klamath River Basin—causes of decline and strategies for recovery*. Washington, D.C.: The National Academies Press.
- Quinn SP, Ross MR. 1982. Annulus formation by white suckers and the reliability of pectoral fin rays for ageing them. *North American Journal of Fisheries Management* 2:204–208.
- Quist MC, Pegg MA, DeVries DR. 2012. Age and growth. Pages 677–731 in Zale AV, Parrish DL, Sutton TM, editors. *Fisheries techniques*. 3rd edition. Bethesda, Maryland: American Fisheries Society Press.
- Radford DS, Lackmann AR, Moody-Carpenter CJ, Colombo RE. 2021. Comparison of four hard structures including otoliths for estimating age in blue suckers. *Transactions of the American Fisheries Society* 150:514–527.
- Scoppettone GG. 1988. Growth and longevity of the Cui-ui and longevity of other Catostomids and Cyprinids in Western North America. *Transactions of the American Fisheries Society* 117:301–307.
- Simmons BR, Beckman DW. 2012. Age determination, growth, and population structure of the striped shiner and duskystripe shiner. *Transactions of the American Fisheries Society* 141:846–854.
- Smith J. 2014. Age validation of lemon sole (*Microstomus kitt*), using marginal increment analysis. *Fisheries Research* 157:41–46.
- Smith M, Von Bargen J, Smith C, Miller M, Rasmussen J, Hewitt DA. 2020. Characterization of the genetic structure of four sucker species in the Klamath

- River—final report. Longview, Washington: U.S. Fish and Wildlife Service, Abernathy Fish Technology Center (see *Supplemental Material*, Reference S15).
- Strickland PA, Middaugh CR. 2015. Validation of annulus formation in spotted sucker otoliths. *Journal of Fish and Wildlife Management* 6:208–212.
- Sylvester RM, Berry CR Jr. 2006. Comparison of white sucker age estimates from scales, pectoral fin rays, and otoliths. *North American Journal of Fisheries Management* 26:24–31.
- Terwilliger MR, Reece T, Markle DF. 2010. Historic and recent age structure and growth of endangered Lost River and Shortnose suckers in Upper Klamath Lake, Oregon. *Environmental Biology of Fish* 89:239–252.
- [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/sites/default/files/documents/endangered-species-act-accessible.pdf> (April 2022)
- [USFWS] U.S. Fish and Wildlife Service. 1988. Endangered and threatened wildlife and plants—determination of the status for the Shortnose sucker and Lost River sucker. *Federal Register* 53(137):27130–27134.
- [USFWS] U.S. Fish and Wildlife Service. 2013. Revised recovery plan for the Lost River sucker (*Deltistes luxatus*) and Shortnose sucker (*Chasmistes brevirostris*). Sacramento, California: U.S. Fish and Wildlife Service, Pacific Southwest Region. Available: <https://ecos.fws.gov/ecp/species/5604> (April 2022; see *Supplemental Material*, Reference S16).
- [USGS] U.S. Geological Survey. 2022. USGS water data for the Nation: U.S. Geological Survey National Water Information System database. Available: <https://doi.org/10.5066/F7P55KJN>