Environ Biol Fish (2010) 89:239–252
DOI 10.1007/s10641-010-9679-9

Historic and recent age structure and growth of endangered Lost River and shortnose suckers in Upper Klamath Lake, Oregon

Mark R. Terwilliger · Tamal Reece · Douglas F. Markle

Received: 28 October 2009 / Accepted: 21 June 2010 / Published online: 13 July 2010

Abstract Seventy-four lapilli from Lost River suckers captured in Upper Klamath Lake in 1970 during a snag fishery on spawning adults and 192 lapilli from adults sacrificed from 2001–2006 were examined to determine age and growth parameters; lapilli from 165 shortnose suckers sacrificed from Upper Klamath Lake from 2001–2006 were also examined. Relative marginal distance analyses indicated that growth marks were annuli and formed in December–January. Lost River suckers from the historic collection were aged to 57 years, while Lost River and shortnose suckers from the recent collection were aged to 40 years and 24 years, respectively. Larger and older Lost River suckers were represented in the historic collection compared to the recent collection. Uncoupling of otolith length and fish length in Lost River suckers as well as a large spread in the predicted age- at-size for shortnose suckers precluded the ability to back-calculate size-at-age. Likelihood ratio tests indicated the growth model parameters were significantly different at both the sex and collection level. Growth in body length for both species appeared determinate in that growth was rapid until maturity, and then slowed over several years until growth in length was nearly nonexistent; a 650–700 mm Lost River sucker could be between 14 and 57 years old, while a 460 mm shortnose sucker could range from 12–24 years old. In contrast, while growth in body length slowed for both species, body mass continued to increase. This growth strategy, which is also found in other western lake suckers, may allow for more energy to be utilized for reproduction and help populations persist in spite of years of limited recruitment or recruitment failure.

Keywords Age · Growth · Upper Klamath Lake · Lost River Sucker · Shortnose sucker

Tamal Reece is deceased

M. R. Terwilliger (✉) · T. Reece · D. F. Markle
Department of Fisheries and Wildlife,
Oregon State University,
104 Nash Hall,
Corvallis, OR 97331-3803, USA
e-mail: terwillm@ucs.orst.edu

Introduction

The Lost River sucker, *Deltistes luxatus*, and the shortnose sucker, *Chasmistes brevirostris*, are large, long-lived catostomids endemic to the Upper Klamath Basin of southern Oregon and northern California (Moyle 2002). They are usually described as obligatory lake-dwellers, and the primary refuge for both species is Upper Klamath Lake in south-central Oregon (Perkins et al. 2000a). Although historically abundant, both species were listed as endangered

(USFWS 1988) because of ageing and declining populations, apparently caused by recruitment failure since the early 1970s. These population declines have been linked to several factors, including: high fishing pressure on spawning adults (Bienz and Ziller 1987); land use practices in the area, such as water diversions, habitat reduction, and poor water quality associated with agricultural and timber practices around the lake and its tributaries; hybridization; and competition with and predation by exotic species (USFWS 1988).

Historically, both species were so abundant in the Upper Klamath Basin that adults were utilized in both a subsistence fishery by the Klamath and Modoc tribes as well as in a popular sport "snag" fishery on spawning adults that began in the early 1900s and peaked in the 1960s and 70s (primarily *D. luxatus,* but also including *Ch. brevirostris,* and to a lesser extent the Klamath largescale sucker, *C. snyderi*) (Markle and Cooperman 2002). Fishing effort was concentrated in three primary areas: in-lake springs, the Williamson River at Highway 97, and the Sprague River at Chiloquin (Fig. 1). The in-lake fisheries were located in the northwest part of the lake at Harriman Springs and at springs along the eastern shore. According to regional newspapers, sport fishermen snagged an estimated 50 tons of suckers (approximately 12,500 fish) during spawning runs in the Williamson and Sprague Rivers during a three-week period in 1966 (Markle and Cooperman 2002). Golden (1969) reported entire pickup trucks loaded with fish as common occurrences. After several years of declining catches (NRC 2004) and elimination of spawning groups (Andreasen 1975), the Klamath Basin Interagency Working Group conducted surveys in the mid-1980s that indicated negligible recruitment to spawning populations (Bienz and Ziller 1987; Scoppettone and Vinyard 1991). Further, opercle age data collected from Lost River suckers after an unexplained 1986 fish kill showed that no substantial recruitment had occurred during the previous 18 years, with 95% of the fish aged at between 19 and 35 years (Scoppettone and Vinyard 1991; NRC 2004); only seven shortnose suckers, aged four to 20 years, were collected (Scoppettone and Vinyard 1991). These data prompted the state of Oregon to close the sport fishery in 1987.

Although Lost River and shortnose suckers were listed over 20 years ago, most of the information available on adult ages of both species came from opercles collected during three substantial lake-wide fish kills (1995–1997), caused by low dissolved oxygen levels exacerbated by bacterial infection (USFWS 2001). Data from these kills indicated that most of the fish were born after closure of the sport fishery; therefore, the age distributions were truncated compared to historic distributions, with most fish under 10 years old (Markle and Cooperman 2002). Conservative estimates placed the number of suckers killed during these three years at 8800 fish (USFWS 2001), a number comparable to those reported annually during the snag fishery in the early 1980s (Markle and Cooperman 2002). The removal of these large, old fish from the population has likely been detrimental to both species. As a group, western lake suckers are characterized by 30–40+ year life spans, late maturation (between ages 4–10 years), high fecundity and iteroparity (Cooke et al. 2005). This life history strategy ensures that reproductive output is allocated across many years, ensuring some reproductive success despite periods that may be unsuitable for larval and juvenile survival (Leaman and Beamish 1984). Broad age distributions may also reduce recruitment variability, as there may be age-related differences in spawning times and locations (Lambert 1987) which could span a wider range of environmental conditions favorable for larval survival (Berkeley et al. 2004a). Removal of large adults from the spawning populations reduced the reproductive potential of the species, created a bottleneck that restricted growth of the sucker populations (NRC 2004), and coupled with poor recruitment due to unfavorable environmental conditions, had imperiled both sucker species. In 2005, an Independent Scientific Review Panel (established as required by the Endangered Species Act) identified significant and sharp population declines and lack of recruitment as current applicable threats to both species (Cascade Quality Solutions 2005).

The age distributions of populations are fundamental indicators of their status. This work represents the first study of age, growth, and longevity for populations of adult and sub-adult Lost River and shortnose suckers based on age estimates from sectioned otoliths, and contributes to the overall knowledge of both historic and recent populations. The objectives of this study were to determine if these species could be aged using lapillar otoliths, and, if so, to provide information on age structure, growth, and longevity of Lost River and shortnose sucker populations from Upper Klamath Lake and its tributaries, and to compare age and growth data between historic and recent collections of Lost River suckers.

Methods

Lapillar otoliths used in this study came from two sources, one of which will be referred to as historic and the other as recent. The historic collection, made by the Oregon Department of Fish and Wildlife (ODFW) in 1970, consisted of lapilli and biological data from 94 Lost River suckers sampled during a creel survey of the snag fishery over three days (April 11, 15 and 17) at two snagging sites (on the Williamson River near the Highway 97 bridge and Sprague River at Chiloquin, Fig. 1). Otoliths from 74 fish that had accompanying length and sex data were analyzed (Table 1). The recent collection was made available to us by the United States Geological Survey (USGS), which collected lapilli and biological data from 192 Lost River suckers and 165 shortnose suckers during sampling in Upper Klamath Lake from 2001–2006 (Table 1). Capture methods used by USGS included trammel netting in the northern section of Upper Klamath Lake, the lower Williamson River, and east-side spring areas as well as sampling the Sprague River fish ladder by trammel and dip net (Fig. 1); see Janney et al. (2008) for gear specifications and methods. Although both data sets are assumed to be representative of the age structure of spawning adults at the time of collection, comparison of age-class structure between the historic and recent samples must be done with caution. ODFW notes indicated that fishers in 1970 discarded smaller fish and lost or broke tackle on larger fish (Bill Tinniswood, ODFW, pers. comm.), and no fish analyzed were captured at shoreline springs. Recent otolith samples came from suckers that were somewhat longer in length than that of the sampled populations in 2003 and 2005 and somewhat smaller in length than sampled populations in 2006. Both sample sets appear to have some unknown size bias with the 1970 samples probably more strongly biased towards larger fish.

We selected the right lapillus for all analyses; however, in a few cases where the right lapillus was damaged or missing, the left lapillus was used. Lapilli were embedded in epoxy resin (Spurr 1969) and a 1.0 mm-thick oblique section running anterodistal-posteromedial that included the core was made using a Buehler Isomet low-speed saw with a diamond-tipped wafering blade. An oblique section was necessary because the main growth axis of the lapillus projects ventrally, the core is not centrally located, and the longest axis of the lapillus sits at an oblique angle relative to the head of the fish. Sections were mounted on glass slides using Crystal Bond adhesive, sanded with 600-grit wet/dry sandpaper to remove saw marks and gain proximity to the core, and polished on a felt pad with 0.5 μm alumina powder. The otolith was flipped several times during grinding and polishing to create a thin section showing visible increments from core to edge (see Secor et al. 1992).

Otolith sections were digitally photographed with a Leica DFC320 digital camera attached to a Leitz Biomed compound microscope, with transmitted light under 40× magnification. These digital images allowed for repeated annuli counts and measurements for precision estimates. Ages were assigned from counts of growth increments that were comprised of a wide translucent and narrow opaque band, and all fish were assigned a nominal birthdate of 1st January. Annuli were counted and measured to the nearest 0.0001 μm using Image Pro Plus 6.0 (2006) software. Due to the curvature of the posterior edge of the otolith and the location of the more “centralized” core, a single measuring path from core to edge would not be perpendicular to all annuli. Therefore, two measurement paths were used: the first was a path perpendicular from the core to the 4th increment, and the second was shifted towards the distal edge and ran perpendicularly from the 4th increment to the ventral edge (Fig. 2). An otolith radius was determined by summing the increment widths measured along these two growth axes.

Within-reader precision was estimated in terms of absolute percent error as outlined in Beamish and Fournier (1981). Annuli on otoliths from all Lost River and shortnose suckers were counted three times by the senior author. The median age (and increment widths associated with that age) obtained from the three reads was used in all subsequent analyses. Counts and measurements were made over the course of several months without information regarding fish size or capture date.

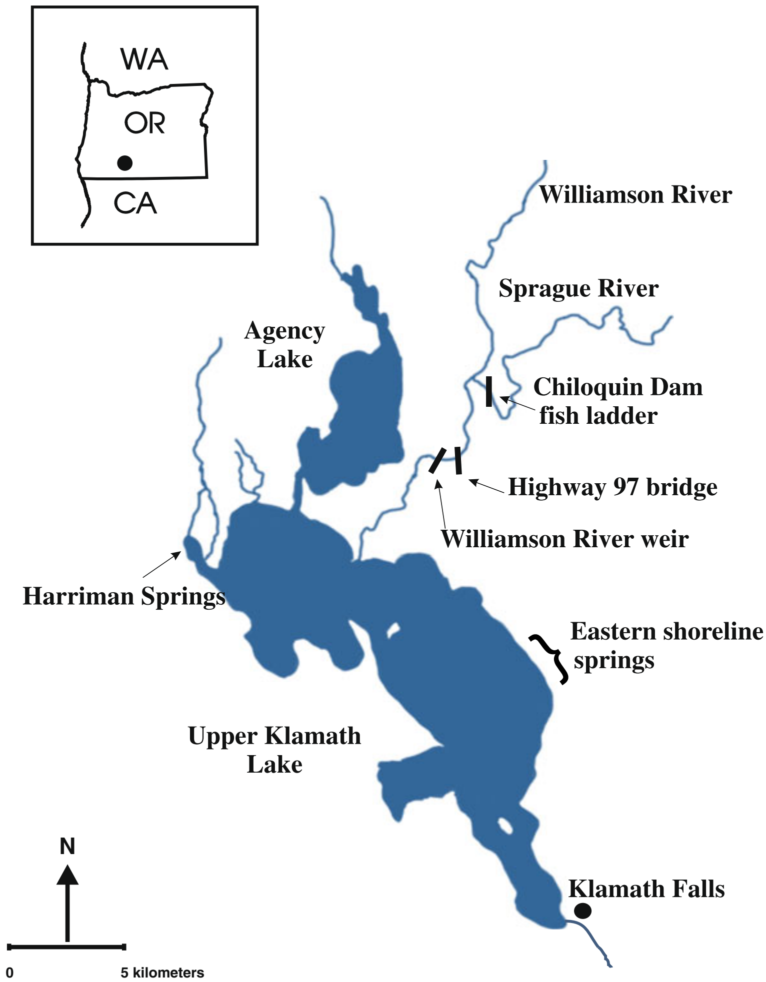

Fig. 1 Map of Upper Klamath Lake and adjoining Agency Lake, Oregon, showing Oregon Department of Fish and Wildlife and U.S. Geological Survey sampling locations for Lost River and shortnose suckers

In his review of age validation methods, Campana (2001) recommended that two procedures be followed when it was not possible to determine absolute age: determination of age at first increment formation and verification of increment periodicity across the entire age range of interest. To validate the age of first increment formation, we measured the distance from core to leading edge in lapilli from randomly selected October-caught age-0 Lost River suckers and shortnose suckers (20 of each species), and assumed that otolith radius in these suckers approximated that of 1-year-old fish. Comparisons of similar measurements were then made to 20 adults from each species. In order to validate the periodicity of growth increment formation, we separated both species into two groups (younger, faster growing individuals and older, slower growing individuals) based upon length-at-age curves (see below), determined the relative marginal distance

Table 1 Numbers of Lost River suckers (LRS) and shortnose suckers (SNS) by sex aged in this study collected in 1970 by Oregon Department of Fish and Wildlife (Historic) and from 2001–2006 by the U.S. Geological Survey (Recent). Five LRS and 1 SNS from the recent collection had no accompanying capture date and were excluded from this table

Year	Historic-LRS			Recent-LRS			Recent-SNS		
	♂	♀	Unk.	♂	♀	Unk.	♂	♀	Unk.
1970	44	29	1						
2001				1	0	0	1	0	0
2002				38	30	4	15	31	6
2003				8	26	0	22	30	3
2004				0	2	0	3	1	0
2005				14	19	0	8	1	0
2006				23	22	0	24	19	0

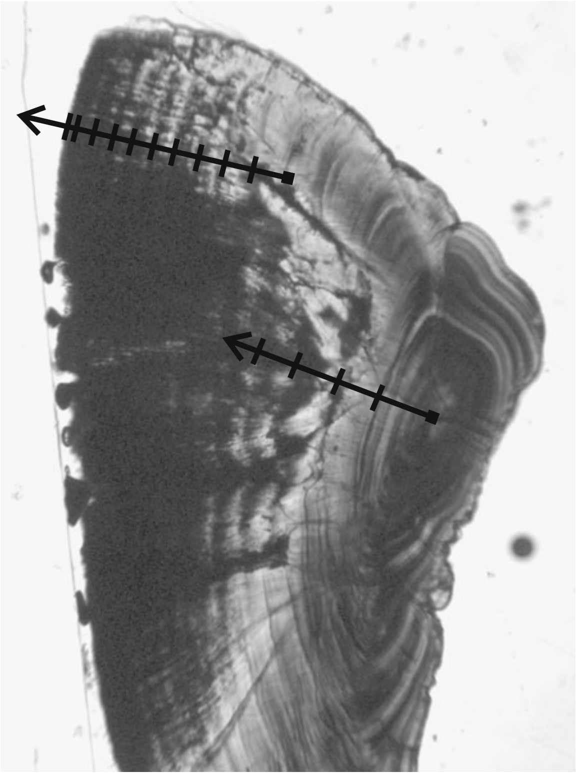

Fig. 2 Oblique section of a lapillus from a 13-year-old Lost River sucker captured in Upper Klamath Lake, Oregon, showing the two paths used for annuli counts and measurements

(RMD), the ratio of the distance from the last growth mark to the edge to the distance separating the last two marks (see Panfili and Morales-Nin 2002), and plotted the mean RMD by month. Lost River and shortnose suckers classified as "younger" had fewer than 12 and 11 growth marks, respectively, on their lapilli. This semi-direct validation technique allowed us to pool otolith measurements into two age categories and accounted for the reduction in growth with age.

To investigate the relationship between otolith size and fish size, we ran general linear models using Statgraphics Centurion statistical software (Statpoint, Inc. 2005) that included sex, fork length, and age as factors. Lost River and shortnose sucker growth were modeled using a two-parameter modification of the von Bertalanffy growth curve in which the size at birth is fixed (Fabens 1965; Neer et al. 2005; Campana et al. 2009):

$$L_t = L_\infty - (L_\infty - L_0)\mathrm{e}^{-Kt},$$

where L_t = predicted length at age t (in years); L_∞ = theoretical asymptotic length; K = rate constant; L_0 = observed length at hatch. We used a mean observed length-at-hatch of 10 mm for Lost River suckers and 8 mm for shortnose suckers as determined by Hoff et al. (1997). Likelihood ratio tests were used to compare von Bertalanffy parameter estimates between collections and sexes of Lost River suckers and between sexes for shortnose suckers (Kimura 1980; Cerrato 1990; Haddon 2001).

Results

Lapilli from 266 Lost River suckers (360–790 mm FL) and 165 shortnose suckers (280–550 mm FL) were examined. Of the Lost River sucker otoliths analyzed, 131 were from females ranging from 387–785 mm FL and 129 were from males ranging from 360–734 mm FL. Six Lost River sucker otoliths had either sex or length data missing. Further analysis of length-at-age (see below) showed that the length data for the 360 mm male Lost River sucker may have had numbers transposed because the data fell approximately six standard deviations from fitted models; this sucker data was therefore excluded from further length-at-age analyses. We found significant differences in fork lengths between historic and recent collections of Lost River suckers (Kolmogorov-Smirnov, p=0.00; Fig. 3) with recently collected Lost River suckers being smaller on average than historic collections. Of the shortnose sucker otoliths, 82 were from females ranging from 283 to 550 mm FL and 74 were from males ranging from 280 to 474 mm FL. Data on length or sex was missing from nine shortnose sucker otoliths. Fork lengths of shortnose suckers were significantly less than those of Lost River suckers collected over the same time period (Kolmogorov-Smirnov, p=0.00; Fig. 3).

Otolith sections displayed well-formed alternating opaque and translucent zones that were easily counted and measured. An average percent error of 1.9% for Lost River suckers and 4.0% for shortnose suckers was estimated, indicating relatively high within-reader precision (see Campana 2001). Oblique sections revealed that otolith structure consisted of an opaque core surrounded by a wide opaque area whose outer edge demarcated the first annulus. The translucent and opaque zones for the following 3–4 annuli were relatively wide and easy to distinguish, and successive annuli were relatively narrow and pronounced.

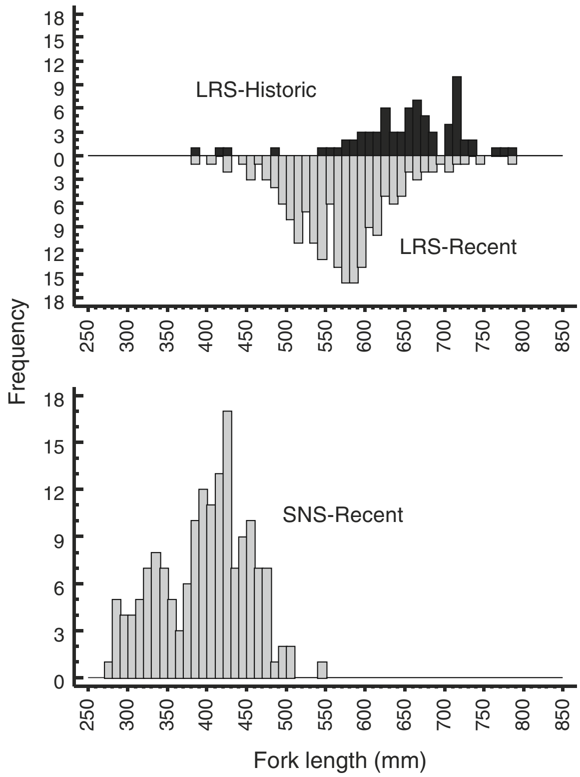

Fig. 3 Length frequency distributions of Lost River suckers (LRS) and shortnose suckers (SNS) captured in Upper Klamath Lake, Oregon, and aged in this study. LRS-Historic refers to suckers collected by Oregon Department of Fish and Wildlife in 1970; LRS-Recent and SNS-Recent refer to suckers collected by the U.S. Geological Survey from 2001–2006

Checks were noted within the first four annuli, but their irregular spacing and contrast made them relatively easy to distinguish from annular marks, which exhibited higher contrast and could be followed along the ventral surface (reference Fig. 2).

When we compared the age at first annulus formation between young-of-the-year and adult suckers, we saw no significant differences in mean lapillar radius at age-1 for either lifestage (t-test; $p=0.11$ and 0.32 for Lost River and shortnose suckers, respectively), corroborating our determination of the first annulus. When we validated periodicity of growth mark formation (Fig. 4), trends were similar for both age groups of both species, with relatively low RMD values occurring early in the calendar year and relatively large RMD values occurring late in the year. Although lake ice-over prevented sampling in December and January, the data were consistent with single, winter growth mark formation, indicating that growth marks were annuli and could be used to age both species.

The oldest Lost River sucker aged in this study was a 57 year old male (673 mm FL) from the historic collection, while the two oldest Lost River suckers from the recent collection were a 40 year old female (708 mm FL) and a 40 year old male of unknown length. The age distribution of Lost River suckers from the recent collection was significantly younger than that of the historic collection (Kolmogorov-Smirnov, $p<0.01$; Fig. 5). The oldest shortnose sucker, from the recent collection, was a 24 year old female (505 mm FL). Recently collected shortnose suckers were also relatively younger when compared to recently collected Lost River suckers (Kolmogorov-Smirnov, $p<0.01$; Fig. 5).

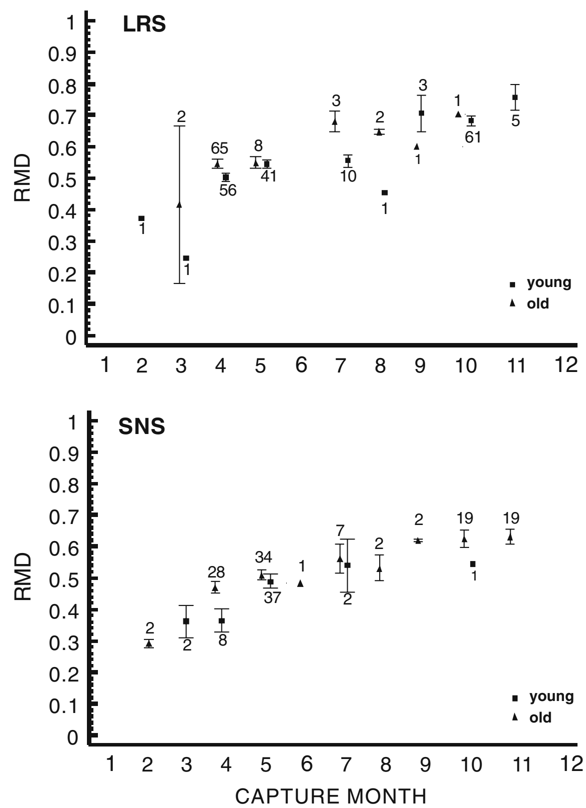

Fig. 4 Mean relative marginal distances (RMD) and associated standard errors plotted by month for young and old Lost River suckers (LRS) and shortnose suckers (SNS). Numbers above and below each point represent sample size. Lost River suckers from historic and recent collections were combined for the analysis. No suckers were captured in Upper Klamath Lake in either collection in January or December; Lost River suckers were also not collected in June

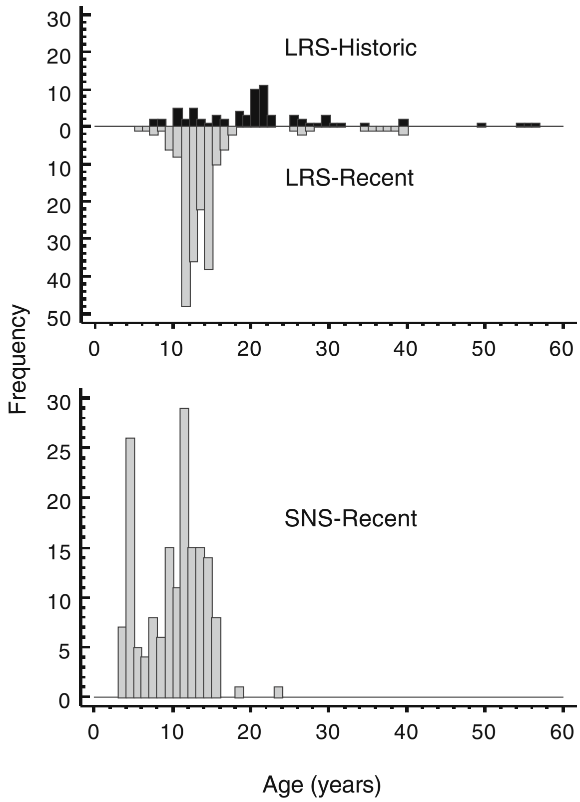

Fig. 5 Age distributions of Lost River suckers (LRS) and shortnose suckers (SNS) captured in Upper Klamath Lake, Oregon, and aged in this study. LRS-Historic refers to suckers collected by Oregon Department of Fish and Wildlife in 1970; LRS-Recent and SNS-Recent refer to suckers collected by the U.S. Geological Survey from 2001–2006.

A strong relationship but trivial effect (small slope) existed between otolith length and fish length for Lost River suckers (ANOVA, $p<0.01$) when sex and age were accounted for in a general linear model (ANOVA, $p=0.0023$ and 0.0000 for sex and age, respectively; Table 2; Fig. 6): a 400 mm fish could have the same otolith length as a 700 mm fish. The relationship between otolith length and fish length for shortnose suckers was also strong (ANOVA, $p<0.01$) and exhibited a larger effect size than that for Lost River suckers (Fig. 6). Sex was not a statistically significant factor in the shortnose sucker model (ANOVA, $p=0.2583$, Table 2) and was dropped. A much stronger positive relationship existed for both species between otolith length and fish age (ANOVA, $p<0.0001$; Fig. 7). Sex and fork length were significant in the Lost River sucker model (Table 2; ANOVA, $p=0.0023$ and 0.0006 for sex and fork length, respectively), but sex was not significant in the shortnose sucker model (ANOVA, $p=0.2583$ and 0.00 for sex and fork length, respectively).

Likelihood ratio tests indicated that growth model parameters were significantly different between collections and sexes for Lost River suckers and between sexes for shortnose suckers (Table 3), so data were not combined. Female Lost River suckers exhibited higher L_∞ values and lower growth coefficient values than males in both historic and recent collections (Table 4). Growth in body length of male and female Lost River suckers from the historic sample was relatively rapid until maturity (age 7–9), slowed for several years post-maturity, and essentially ceased over the remaining 40 years of life (Fig. 8). Although the age structure was truncated compared to the historic sample, Lost River suckers from the more recent collection exhibited similar traits in growth over the first 16 years of life, with growth in body length essentially ceasing over the last few years of life. In contrast, body mass continued to increase with age up to about age 30 in both sexes (Terwilliger,

Table 2 ANOVA table summarizing results of fitting a general linear statistical model relating Lost River sucker (LRS) and shortnose sucker (SNS) otolith length (OL) to predictive factors of sex, fork length (FL), and age. DF = degrees of freedom

Model	Source	Sum of Squares	DF	Mean Square	*F*-Ratio	*P*-Value
LRS-OL	Sex	137608.0	2	68804.1	6.22	0.0023
	FL	132140.0	1	132140.0	11.94	0.0006
	Age	1.95×10^7	1	1.95×10^7	1760.80	0.0000
	Residual	2.83×10^6	256	11069.1		
	Total (corrected)	3.88×10^7	260			
SNS-OL	Sex	15246.7	2	7623.36	1.37	0.2583
	FL	94436.3	1	94436.3	16.92	0.0001
	Age	3.03×10^6	1	3.03×10^6	542.12	0.0000
	Residual	865209.0	155	5582.0		
	Total (corrected)	1.38×10^7	159			

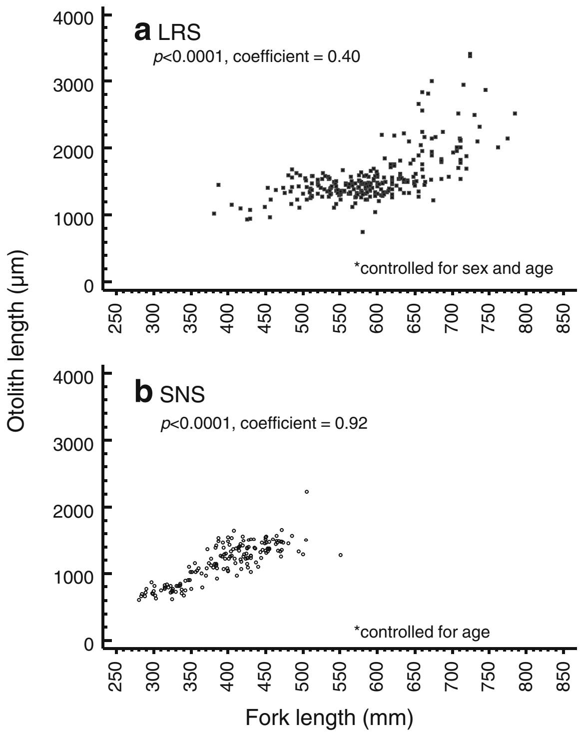

Fig. 6 Scatterplots of otolith length on fork length for (a) Lost River suckers (LRS) and (b) shortnose suckers (SNS). LRS from historic and recent collections were combined for the analyses

unpubl. data). Male and female Lost River suckers achieved 50% of L_∞ by age 6 and 75% between ages 10 and 11 (Fig. 8). Longevities of Lost River suckers from both collections were similar between sexes.

Male and female shortnose sucker growth in body length was relatively rapid until age 5 before slowing over the next six years and essentially ceasing for ages greater than 11 years (Fig. 9). This reduction in growth rate occurred at an age coinciding with the onset of maturity for this species. Male and female shortnose suckers achieved 50% of L_∞ by age 3 and 75% between ages 5 and 6 (Fig. 9). Female shortnose suckers exhibited greater longevity than males (24 years and 19 years for females and males, respectively), and like Lost River suckers, exhibited higher L_∞ values and lower growth coefficient values than males (Table 4).

Rarefaction of both historic and recent samples (Fig. 10) showed that the recent sample was represented by fewer year-classes of Lost River suckers than the historic sample, and curves showed no evidence of crossing. Lost River suckers from the historic collection were represented by 27 year classes ranging from 1913 to 1962 (Fig. 11), with two relatively strong year classes (1948 and 1949) accounting for 28% of the sample. The Lost River sucker birthyear distribution from the recent collection was truncated compared to the historic sample, and was represented by 21 year classes ranging from 1963 to 1999 (Fig. 11), with two relatively strong year classes (1990 and 1991) accounting for 55% of the sample. Shortnose suckers from the recent collection were represented by 15 year classes ranging from 1979 to 2000 (Fig. 11), with two periods of relatively strong year classes: 1990–1991, which accounted for 35% of the sample, and 1998, which accounted for nearly 20% of the sample.

Discussion

This study represents the first attempt at ageing adult and sub-adult Lost River and shortnose suckers using otoliths. High precision estimates and the results of RMD analyses support the use of lapilli for ageing adults and sub-adults of both species. Previous attempts

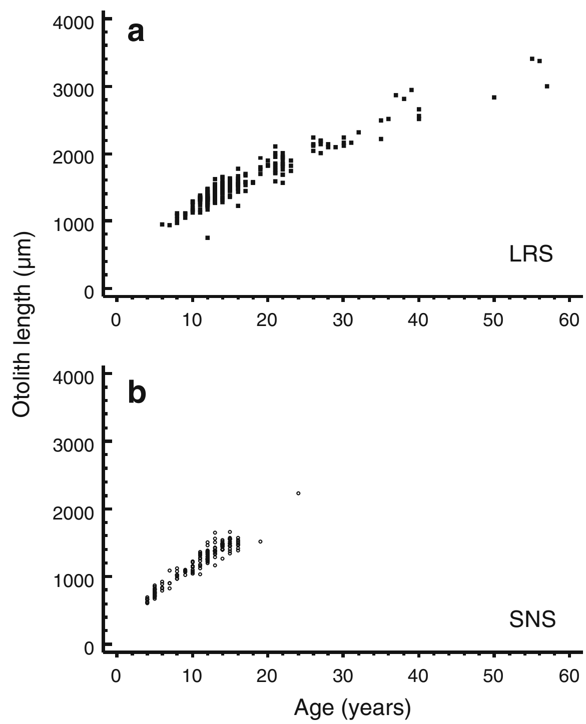

Fig. 7 Scatterplots of otolith length on age for (a) Lost River suckers (LRS) and (b) shortnose suckers (SNS). LRS from historic and recent collections were combined for the analyses

Table 3 Likelihood ratio tests comparing von Bertalanffy parameter estimates between historic (h) and recent (r) collections of Lost River suckers (LRS), and between male (1) and female (2) Lost River and shortnose suckers (SNS) from each collection

Comparison	Hypothesis	Linear constraints	RSS	χ_r^2	df	*P*
LRS: Historic vs. Recent	H_Ω	none	660294.10			
	$H_{\omega 1}$	$L_{\infty h}=L_{\infty r}$	661632.97	0.5226	1	0.470
	$H_{\omega 2}$	$K_h=K_r$	664014.33	1.4495	1	0.229
	$H_{\omega 3}$	$L_{\infty h}=L_{\infty r}$ $K_h=K_r$	702908.24	16.13558	2	0.000
LRS Historic: male vs. female	H_Ω	none	128375.96			
	$H_{\omega 1}$	$L_{\infty 1}=L_{\infty 2}$	162547.99	17.2287	1	0.083
	$H_{\omega 2}$	$K_1=K_2$	133761.06	2.9997	1	0.000
	$H_{\omega 3}$	$L_{\infty 1}=L_{\infty 2}$ $K_1=K_2$	176447.72	23.2185	2	0.000
LRS Recent: male vs. female	H_Ω	none	441228.67			
	$H_{\omega 1}$	$L_{\infty 1}=L_{\infty 2}$	459212.58	7.3907	1	0.007
	$H_{\omega 2}$	$K_1=K_2$	449732.07	3.5314	1	0.060
	$H_{\omega 3}$	$L_{\infty 1}=L_{\infty 2}$ $K_1=K_2$	483846.38	17.0578	2	0.000
SNS: male vs. female	H_Ω	none	118090.52			
	$H_{\omega 1}$	$L_{\infty 1}=L_{\infty 2}$	131884.85	17.2045	1	0.000
	$H_{\omega 2}$	$K_1=K_2$	119328.45	1.6268	1	0.202
	$H_{\omega 3}$	$L_{\infty 1}=L_{\infty 2}$ $K_1=K_2$	146075.12	33.1765	2	0.000

at ageing these species included the use of scales and opercular bones (Scoppettone 1988); however, scales are notorious for underestimating age in long-lived species, and ages from opercula may also underestimate true age. Researchers (Scoppettone 1988; Peterson et al. 1999) have described the presence of hidden annuli on catostomid opercular bones due to fenestrated reinforcement bone immediately ventral to the hyomandibular socket, the number of which was a function of the age and shape of the opercle. In contrast, lapilli for these species are easily prepared for reading, growth marks are annular, and checks are relatively easy to distinguish from true annuli. Further support for using lapilli to age catostomids was supplied by Sylvester and Berry (2006), who determined that the lapillus was the preferred hard part for ageing populations of white sucker, *Catostomus commersonii*; further, Thompson and Beckman (1995) used edge analysis to determine that marks on lapilli were annular for that species. Belk (1998) also reported unvalidated ages from June sucker (*Chasmistes liorus*) lapilli.

The maximum age of Lost River suckers aged in this study was 57 years, which is 14 years older than the previously published maximum age for the species, and came from a relatively small sample. Previous ageing of Lost River suckers was performed by Scoppettone (1988) and by Coleman et al. (1988), who examined opercles from fish collect-

Table 4 Calculated von Bertalanffy parameters for male and female Lost River suckers (LRS) collected in 1970 by the Oregon Department of Fish and Wildlife (Historic) and from 2001–2006 by the U.S. Geological Survey (Recent), and for male and female shortnose suckers (SNS) from recent collections. Jackknifed standard errors are in parentheses

Parameter	Historic		Recent			
	LRS ♂	LRS ♀	LRS ♂	LRS ♀	SNS ♂	SNS ♀
L_∞	663.16 (10.41)	742.44 (19.73)	608.42 (23.50)	700.58 (22.82)	424.50 (6.18)	464.32 (7.07)
K	0.169 (0.020)	0.133 (0.028)	0.179 (0.028)	0.130 (0.013)	0.266 (0.013)	0.237 (0.015)
n	44	29	84	101	74	82

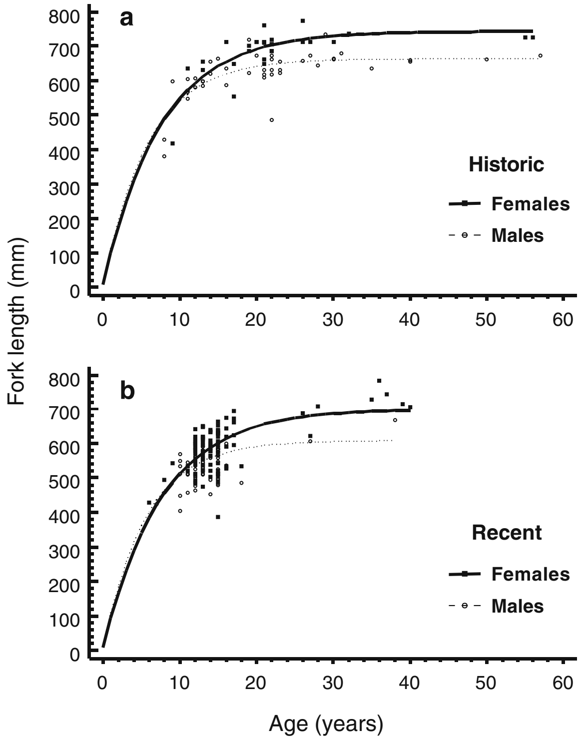

Fig. 8 Two-parameter von Bertalanffy growth curves for Lost River suckers for varying combinations of sex and collection: (a) female (solid line) and male (dashed line) Lost River suckers from the historic collection; (b) female (solid line) and male (dashed line) Lost River suckers from the recent collection

ed during the 1986 fish kill in Upper Klamath Lake. Both authors determined a maximum age of 43 years, but decomposition precluded accurate length measurements and/or sex determinations on many fish so length-at-age could not be determined. This age difference between historic Lost River suckers aged

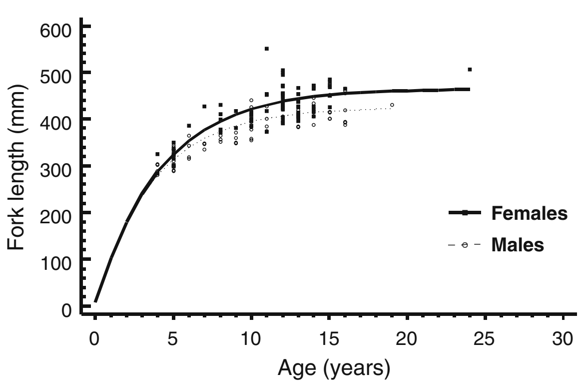

Fig. 9 Two-parameter von Bertalanffy growth curves for female (solid line) and male (dashed line) shortnose suckers from the recent collection

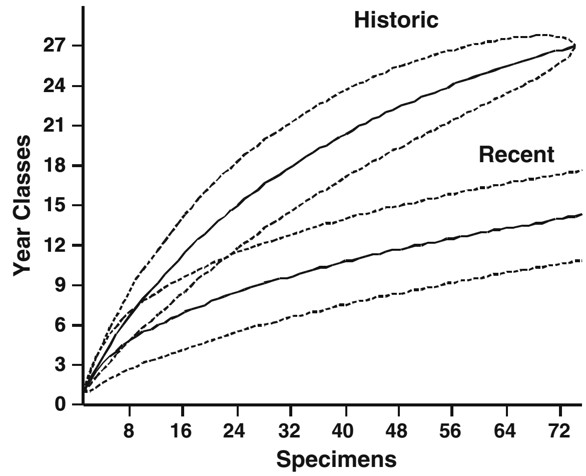

Fig. 10 Rarefaction curves (solid lines) and 95% confidence intervals (dashed lines) for Lost River suckers from historic and recent collections

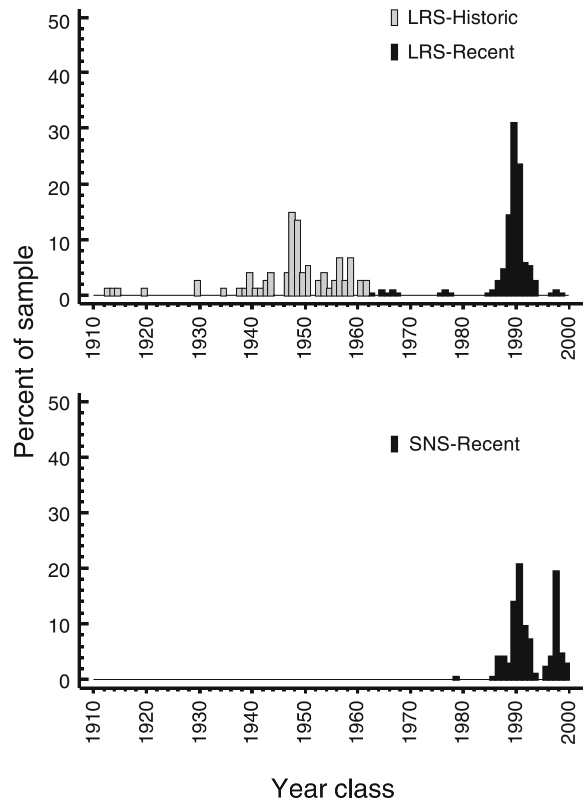

Fig. 11 Age distribution (by year class) of Lost River suckers from the historic (LRS-Historic) and recent (LRS-Recent) collections and shortnose suckers from the recent (SNS-Recent) collections

in this study and the 1986 fish kill data may be due to decades of intense fishing pressure on large spawning adults that reduced the number of large, old adults in Upper Klamath Lake. Age truncation in fished populations is known to occur even at moderate levels of exploitation, and is especially detrimental to long-lived, iteroparous species that exhibit highly variable reproductive success, as populations consisting of a broad spectrum of age classes may be better able to buffer environmental events (Berkeley et al. 2004b; Hsieh et al. 2006).

Lost River suckers aged from the 1986 fish kill ranged from 8 to 43 years of age, with most fish (90%) aged 19 to 28 years, indicating a general lack of recruitment over the previous two decades (Coleman et al. 1988). This lack of recruitment further explains the age and length distributions of recently collected Lost River suckers reported in this study. The maximum age seen in the recent collection was 40 years, corresponding to an approximate 20-year-old fish from 1986. The majority of recently captured Lost River suckers aged in this study were between 9 and 18 years, corresponding to birthdates occurring after the close of the snag fishery and the 1986 fish kill. The maximum age of shortnose suckers aged in this study was 24 years, much younger than previously reported maximum ages of 33 years for fish from Copco Reservoir, California (Scoppettone 1988). Nine shortnose suckers collected during the 1986 fish kill were aged from 4 to 20+ years, with 5 fish aged 19+ (Coleman et al. 1988), indicating that recruitment may also have been poor over the two decades prior to the kill as well. Unfortunately, ODFW sampled no shortnose suckers in the 1970's snag fishery for comparison with contemporary samples.

The two-parameter modified von Bertalanffy growth curves fit the observed data well and resulted in realistic estimates of L_∞ and K for males and females of both species. We initially attempted to fit the generalized 3-parameter version of the von Bertalanffy growth curve to the data (containing estimates of L_∞, K, and the theoretical age at zero length, t_0), but the lack of fish at younger ages prevented the three-parameter model from producing biologically reasonable estimates of t_0 and L_0, the observed length at hatch. The two-parameter model also provided more biologically realistic estimates of juvenile growth for both species than did the three-parameter von Bertalanffy model.

One of the main products of any ageing study is a determination of back-calculated size-at-age. It is often assumed that otolith growth is dependent upon somatic growth, and virtually all growth back-calculation procedures are dependant upon some proportionality between otolith size and fish size (Carlander 1981). The assumption that somatic growth and otolith growth are coupled has been determined false in a number of studies (Reznick et al. 1989; Wright et al. 1990; Hare and Cowen 1995). In this study, we found that otolith length was a poor predictor of fish length for Lost River suckers (Fig. 6). This was especially true for relatively larger fish >650 mm FL. In effect, the lapilli continued to grow even as body length growth slowed down or ceased. This uncoupling of otolith and fish length precluded the use of increment width data to back-calculate size-at-age for adults and sub-adults of this species. Instead, otolith size was a strong predictor of age; older fish had larger otoliths. This trend of decoupled growth was also seen in shortnose suckers, but because of the truncated age structure (compared to Lost River suckers), the trend was not as apparent. Still, for shortnose suckers, the data showed an otolith size range of several hundred microns for fish >380 mm FL (Fig. 6). Further, the absence of younger, smaller fish in our samples precluded the use of proportional back-calculation methods (see Francis 1990). Even if we assumed that proportionality between body size and otolith size began for lengths of the smallest fish at hand (and used the biological intercept method, see Campana 1990), there is a large (6–7 year) spread in the prediction limits of age at back-calculated size for fish represented in the samples, so the predictive value in back-calculating length-at-age is severely diminished. Upper Klamath Lake suckers, especially Lost River suckers, exhibited determinate growth in body length, where growth was rapid prior to maturity, intermediate for several years after maturity, and then slowed to almost no growth in older fish. However, increase in body mass continued to about age 30. This rapid reduction in body length growth after maturity to little or no growth over several decades accounts for the fact that, although we aged fish captured by a variety of size-selective gears in differing locations around Upper Klamath Lake over varying time periods, there is little influence of size bias on age for most size ranges sampled. Fish length is a poor predictor of otolith size and age for Lost River suckers (Figs. 6, 8) and fish length is a poor predictor of age for shortnose suckers (Fig. 9).

This growth pattern is similar to other western lake suckers, including the cui-ui (*Ch. cujus*), June sucker (*Ch. liorus*), and razorback sucker (*Xyrauchen texanus*). Scoppettone (1988) showed that cui-ui from Pyramid Lake, Nevada, exhibited rapid growth to age 10 followed by little to no growth in body length over the subsequent 32 years of the species' life span. Belk (1998) aged only 10 June suckers from Utah Lake, Utah, and noted a 24-year age difference in fish that were essentially the same length. The rapid increase in body length to maturation, followed by growth in body mass rather than length over a long reproductive lifespan, allows for more energy to be utilized for reproduction and helps western lake sucker populations to persist in spite of years of limited recruitment or recruitment failure (Belk 1998; Berkeley et al. 2004a). Data for Lost River suckers reinforces this point. Although there are strong limitations based on essentially two non-random snapshot samples, each data set had only one relatively strong recruitment period, between 1–2 decades prior to the sample (Fig. 10). Ageing studies on cui-ui (Scoppettone 1988) and razorback sucker (McCarthy and Minckley 1987) have also demonstrated persisting populations despite 18-year and 30-year droughts in recruitment for those species.

Age distributions by year class of Lost River and shortnose suckers aged in this study (Fig. 11) indicate correspondence of renewed recruitment with closure of the sport fishery in 1987. Although age samples were haphazard and the 1970 samples could not have detected them, none of the available age data provide evidence of Lost River sucker recruitment from 1968 to 1988. The 1986 fish kill data showed 95% were born before 1967 (Scoppettone and Vinyard 1991). In contrast, the 1995–1997 fish kill data showed almost all were born after 1987 (Markle and Cooperman 2002; NRC 2004). Assuming different fish kills do not have differential size bias, both data sets should have detected production from 1968 to 1988. Those decades of low recruitment, to be expected in a long-lived species, were coincident with and may have been exacerbated by the fishery.

Although we aged no historic shortnose suckers, the age distribution of the recently captured shortnose suckers mirrors that of Lost River suckers, with few fish born prior to closure of the fishery. The larger, older spawners that were typically targeted in the snag fishery are known to produce more gametes than smaller, younger suckers (Buettner and Scoppettone 1990; Perkins et al. 2000b), and may produce more fit eggs and larvae which might better survive to recruit to the adult population (Hislop 1988; Berkeley et al. 2004a). The long-lived, iteroparous life history strategy seen in these species makes them susceptible to overexploitation, and the snag fishery reduced the number of old spawners and subsequently lowered per capita egg production (Markle and Cooperman 2002). After listing, populations of both species exhibited a transition from older, larger individuals to primarily smaller, recruit-sized individuals by the late 1990s indicating recruitment into the spawning populations (Janney et al. 2008). Unfortunately, the fish kills of the mid-90s coincided with the time when the strong year classes from the early 1990s would have been expected to begin spawning (Markle and Cooperman 2002), and the percentage of recruit-sized suckers in spawning runs has steadily declined over the decade since (Janney et al. 2008). In fact, it has been estimated that spawning populations of both species were reduced between 80–90% from 1995 to 1998 (USFWS 2002; NRC 2004). Although, as a group, western lakesuckers are characterized by 30–40 year lifespans, a recent demographic analysis of Klamath sucker spawning populations from 1995–2006 revealed low annual survival probabilities and average reproductive lifespans of only 8 years for Lost River suckers and 3.6 years for shortnose suckers (Janney et al. 2008). Lethal research take for ageing structures may need to be recognized as a cause for concern and non-lethal alternatives explored.

Acknowledgements We are grateful to Eric Janney and Scott Vanderkooi, U.S. Geological Society, Klamath Falls field office, for providing recent otoliths for this study. Authorizations for recent collections were under Federal permit TE007907 and Oregon State permits OR2001-010, OR2002-022, OR2003-1033, OR2004-1793, OR2005-2538, and OR2006-3241. Ariel Muldoon (OSU) provided statistical assistance and Bill Tinniswood, Oregon Department of Fish and Wildlife, shared creel notes from the snag fishery. Steve Campana provided insights on the validation technique and growth modeling. Finally, we wish to acknowledge the work of our late student and coauthor, Tamal Reece, whose meticulous work enhanced this study and whose untimely death cut short his future contributions.

References

Andreasen JK (1975) Systematics and status of the family Catostomidae in southern Oregon. Dissertation, Oregon State University

Beamish RJ, Fournier DA (1981) A method for comparing the precision of a set of age determinations. Can J Fish Aquat Sci 38:982–983

Belk MC (1998) Age and growth of June sucker (*Chasmistes liorus*) from otoliths. Gt Basin Nat 58(4):390–392

Berkeley SA, Chapman C, Sogard SM (2004a) Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecol 85(5):1258–1264

Berkeley SA, Hixon MA, Larson RJ, Love MS (2004b) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29 (8):23–32

Bienz CS, Ziller JS (1987) Status of three lacustrine sucker species (Catostomidae). Report to the U.S. Fish and Wildlife Service, Sacramento, p 39

Buettner M, Scoppettone GG (1990) Life history and status of catostomids in Upper Klamath Lake, Oregon. Completion Report. U.S. Fish and Wildlife Service, National Fisheries Research Center, Seattle

Campana SE (1990) How reliable are growth back-calculations based on otoliths? Can J Fish Aquat Sci 47:2219–2227

Campana SE (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J Fish Biol 59:197–242

Campana SE, Joyce W, Kulka DW (2009) Growth and reproduction of spiny dogfish off the eastern coast of Canada, including inferences on stock structure. In: Gallucci VF, McFarlane GA, Bargmann GG (eds) Biology and management of dogfish sharks. American Fisheries Society, Bethesda, pp 195–208

Carlander KD (1981) Caution on the use of the regression method of back-calculating lengths from scale measurements. Fish 6:2–4

Cascade Quality Solutions (2005) The current risk of extinction of the Lost River and shortnose suckers. Independent Scientific Review Panel meeting proceedings prepared for U.S. Fish and Wildlife Service, Klamath Falls Field Office, Klamath Falls, p 227

Cerrato RM (1990) Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can J Fish Aquat Sci 47:1416–1426

Coleman ME, Kann J, Scoppettone GG (1988) Life history and ecological investigations of catostomids from the Upper Klamath Basin, Oregon. National Fisheries Research Center, Seattle, p 109

Cooke SJ, Bunt CM, Hamilton SJ, Jennings CA, Pearson MP, Cooperman MS, Markle DF (2005) Threats, conservation strategies, and prognosis for suckers (Catostomidae) in North America: insights from regional case studies of a diverse family of non-game fishes. Biol Conserv 121(3):317–331

Fabens AJ (1965) Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289

Francis RICC (1990) Back-calculation of fish length: a critical review. J Fish Biol 36:883–902

Golden MP (1969) The Lost River sucker. Oregon State Game Commission Central Region Administrative Report 1–69. pp 14

Haddon M (2001) Modeling and quantitative methods in fisheries. Chapman and Hall/CRC, Boca Raton

Hare JA, Cowen RK (1995) Effect of age, growth rate, and ontogeny on the otolith size-fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. Can J Fish Aquat Sci 52:1909–1922

Hislop JRG (1988) The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. J Fish Biol 32:923–930

Hoff GR, Logan DJ, Markle DF (1997) Otolith morphology and increment validation in young Lost River and shortnose suckers. Trans Am Fish Soc 126:488–494

Hsieh C-h, Reiss CS, Hunter JR, Beddington RM, Sugihara G (2006) Fishing elevates variability in the abundance of exploited species. Nature 443:859–862

Janney EC, Shively RS, Hayes BS, Barry PM (2008) Demographic analysis of Lost River sucker and shortnose sucker populations in Upper Klamath Lake, Oregon. Trans Am Fish Soc 137:1812–1825

Kimura DK (1980) Likelihood methods for the von Bertalanffy growth curve. Fish Bull 77:765–775

Lambert TC (1987) Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the population. Mar Ecol Prog Ser 39:209–220

Leaman BM, Beamish RJ (1984) Ecological and management implications of longevity in some northeast Pacific groundfishes. Int N Pac Fish Comm Bull 42:85–97

Markle DF, Cooperman M (2002) Relationships between Lost River and shortnose sucker biology and management of Upper Klamath Lake. In: Braunworth WS Jr, Welch T, Hathaway R (eds) Water allocation in the Klamath Reclamation Project, 2001: An assessment of natural resource, economic, social, and institutional issues with a focus on the Upper Klamath Basin. Oregon State University Extension Service Special Report 1037, Corvallis, pp 93–117

McCarthy MS, Minckley WL (1987) Age estimation for razorback sucker (Pisces: Catostomidae) from Lake Mohave, Arizona and Nevada. J Ariz-Nev Acad Sci 21:87–97

Moyle PB (2002) Inland Fishes of California. University of California Press, Berkeley, 502 pp

Neer JA, Thompson BA, Carlson JK (2005) Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth. J Fish Biol 67:370–383

NRC (National Resource Council) (2004) Endangered and threatened fishes in the Klamath River Basin. The National Academies Press, Washington

Panfili J, Morales-Nin B (2002) Semi-direct validation. In: Panfili J, de Pontual H, Troadec H, Wright PJ (eds) Manual of fish schlerochronology. Ifremer-IRD coedition, Brest, pp 129–134

Perkins DL, Kann J, Scoppettone GG (2000a) The role of poor water quality and fish kills in the decline of endangered Lost River and shortnose suckers in Upper Klamath Lake. U.S. Geological Survey, Biological Resources Division Report submitted to the U.S. Bureau of Reclamation, Contract 4-AA-29-12160, Klamath Falls Project Office, Klamath Falls, OR

Perkins DL, Scoppettone GG, Buettner M (2000b) Reproductive biology and demographics of endangered Lost River and shortnose suckers in Upper Klamath Lake, Oregon. Unpublished manuscript, U.S. Geological Survey, Biological Resource Division, Reno, NV

Peterson MS, Nicholson LC, Snyder DJ, Fulling GL (1999) Growth, spawning preparedness, and diet of *Cycleptus meridionalis* (Catostomidae). Trans Am Fish Soc 128:900–909

Reznick D, Lindbeck E, Bryga H (1989) Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). Can J Fish Aquat Sci 46:108–112

Scoppettone GG (1988) Growth and longevity of the cui-ui and longevity of other catostomids and cyprinids in western North America. Trans Am Fish Soc 117:301–307

Scoppettone GG, Vinyard G (1991) Life history and management of four endangered lacustrine suckers. In: Minkley WL, Deacon JE (eds) Battle against extinction: native fish management in the American West. The University of Arizona Press, Tucson, AZ, pp 359–377

Secor DH, Dean JM, Laban EH (1992) Otolith removal and preparation for microstructural examination. In: Stevenson DK, Campana SE (eds) Otolith microstructural examination and analysis. Can Spec Pub Fish Aquat Sci 117, pp 19–57

Spurr AR (1969) A low-viscosity epoxy resin embedding medium for electron microscopy. J Ultrastruct Res 26:31–43

Statpoint, Inc (2005) The user's guide to Statgraphics® Centurion XV. 287 pp.

Sylvester RM, Berry CR Jr (2006) Comparison of white sucker age estimates from scales, pectoral fin rays, and otoliths. N Am J Fish Manage 26:24–31

Thompson KR, Beckman DW (1995) Validation of age estimates from white sucker otoliths. Trans Am Fish Soc 124:637–639

USFWS (U.S. Fish and Wildlife Service) (1988) Endangered and threatened wildlife and plants; shortnose and Lost River suckers, Houghton's goldenrod and Pitcher's thistle; final rules. U.S. Office of the Federal Register 53 (18 July 1988): 27130–27134

USFWS (U.S. Fish and Wildlife Service) (2001) Biological/conference opinion regarding the effects of operation of the Bureau of Reclamation's Klamath Project on the endangered Lost River sucker (*Deltistes luxatus*), endangered shortnose sucker (*Chasmistes brevirostris*), threatened bald eagle (*Haliaeetus leucocephalus*), and proposed critical habitat for the Lost River/shortnose suckers. USFWS, Klamath Falls Fish and Wildlife Office, Klamath Falls

USFWS (U.S. Fish and Wildlife Service) (2002) Biological/conference opinion regarding the effects of operation of the Bureau of Reclamation's Klamath Project on the endangered Lost River sucker (*Deltistes luxatus*), endangered shortnose sucker (*Chasmistes brevirostris*), threatened bald eagle (*Haliaeetus leucocephalus*), and proposed critical habitat for the Lost River/shortnose suckers. USFWS, Klamath Falls Fish and Wildlife Office, Klamath FallsOregon

Wright PJ, Metcalfe NB, Thorpe JE (1990) Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. J Fish Biol 36:241–149