

Validation of Annulus Formation in Otoliths of Notchlip Redhorse (*Moxostoma collapsum*) and Brassy Jumprock (*Moxostoma* sp.) in Broad River, South Carolina, with Observations on their Growth and Mortality

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Abstract - *Moxostoma collapsum* (Notchlip Redhorse) and the undescribed *Moxostoma* sp. (Brassy Jumprock) form a large component of the fish assemblage in the Broad River, SC, but little is known about their population characteristics, nor has an aging method been validated for either species. We validate that one annulus is formed each year in the lapillus otolith of the two species and identify spring as the period of annulus formation, using chemical marking and marginal increment analyses, respectively. Notchlip Redhorse and Brassy Jumprock are long-lived, with observed maximum estimated ages of 17 and 21, respectively. Both species grow quickly during their first few years; little growth occurs after age 7. Instantaneous total mortality of each species was low ($Z \leq 0.35$), suggesting there is little exploitation of either species in the Broad River, SC.

Introduction

Suckers (Pisces: Catostomidae) represent an important component of the Broad River, SC, fish assemblage, accounting for more than 51% of total fish biomass (Bettinger et al. 2003). Two species, *Moxostoma collapsum* Cope (Notchlip Redhorse) and an undescribed *Moxostoma* sp. (Brassy Jumprock) (Jenkins and Burkhead 1994), are among the most abundant fishes in the river, accounting for more than 12% and 5%, respectively, of the relative abundance of all fish species, and together comprising nearly 90% of the relative abundance of all catostomids (Bettinger et al. 2003). Yet little is known about their age structure, growth, and mortality within the Broad River or in other systems throughout their range. In fact, there is limited published life-history information for catostomids in general. Cooke et al. (2005) suggested that the paucity of available life-history information has hampered conservation efforts for this diverse and ecologically important family.

Notchlip Redhorse was recently removed from synonymy with *Moxostoma anisurum* Rafinesque (Silver Redhorse) (Nelson et al. 2004), which only occurs in the Mississippi basin and northward (Lee et al. 1980). Notchlip Redhorse is an Atlantic Slope species ranging from Georgia to Virginia; its distribution in Lee et al. (1980) is shown as the “southeastern race” of *M. anisurum*. Published information on age and growth of Silver Redhorse is restricted to studies conducted in the Mississippi basin (Hackney et al. 1971, Meyer 1962). Grabowski et al. (2007) estimated the growth of four catostomid species, including Notchlip Redhorse, in the Savannah River, South Carolina–Georgia.

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Brassy Jumprock was formerly known as *Moxostoma robustus* Cope (Smallfin Redhorse). However, Jenkins and Burkhead (1994:491 [footnote]) determined that the species was never described or validly named. While the species remains undescribed at the time of publication, there is general consensus that its common name is Brassy Jumprock (Jenkins and Burkhead 1994). Brassy Jumprock is also an Atlantic Slope species ranging from Georgia to Virginia (Lee et al. 1980:432). We were unable to find any published information on the growth and longevity of either Smallfin Redhorse or Brassy Jumprock.

Several structures have been used to age catostomid species, including scales, fin rays, opercle bones, and otoliths. However, the use of scales and fin rays has been shown to be an unreliable estimator of age in older, mature *Moxostoma erythrurum* Rafinesque (Golden Redhorse; Curry and Spacie 1984) and *Catostomus commersoni* Lacepède (White Sucker; Sylvester and Berry 2006), though fin rays were comparable to otoliths when estimating the ages of *Catostomus discobolus* Cope (Bluehead Sucker), *Catostomus latipinnis* Baird and Girard (Flannelmouth Sucker), and White Sucker in a Wyoming stream (Quist et al. 2007). Otoliths have been used and validated as an appropriate structure for estimating the ages of *Moxostoma carinatum* Cope (River Redhorse; Hutson 1999), *Moxostoma duquesnei* Lesueur (Black Redhorse), Golden Redhorse (Howlett 1999), and White Sucker (Thompson and Beckman 1995). Of the three otolith pairs present, lapilli are preferred for age estimation of catostomids because they are generally larger, more durable, and more readable than sagittae or asterisci (Hoff et al. 1997).

The objectives of this study were to validate yearly annulus formation in the otoliths of Notchlip Redhorse and Brassy Jumprock, determine the season of annulus deposition, and describe the growth, longevity, and mortality of the two species in the Broad River, SC.

Methods

Study area

The Broad River basin is a major division of the Santee River drainage. It originates in North Carolina and dominates the central Piedmont of South Carolina (Fig. 1). Within South Carolina, the Broad River basin encompasses 9819 square km; the river flows approximately 170 km until it merges with the Saluda River, near Columbia, SC, to form the Congaree River. Average annual discharge during 1999–2009, based on mean daily averages, of the Broad River approximately 11 km downstream from the North Carolina state line was 1546 cfs, while average discharge 16 km below Parr Reservoir, near Columbia, SC, was 3912 cfs. Average annual water temperature at Carlisle, SC (mid-length of the river), based on mean daily average was 17.9 °C during 1999 through 2009, and average annual minimum and maximum water temperatures for that period were 2.7 °C and 32.1 °C, respectively.

The Broad River is relatively shallow with few unimpounded areas deeper than 3 m. The majority of the habitat in the river is shallow sand-filled pools

separated by bedrock shoals and gravel riffles. The river is interrupted by seven hydroelectric dams with run-of-the-river impoundments ranging in size from 101 ha to 1781 ha.

Annulus validation

During October 2001, 91 Brassy Jumprock (mean total length [TL] = 321 mm; range = 190–445 mm) and 33 Notchlip Redhorse (mean TL = 399 mm; range = 217–475 mm) were collected from the lower Broad River, below Parr Shoals Reservoir, with boat-mounted electrofishing gear. Each fish was measured

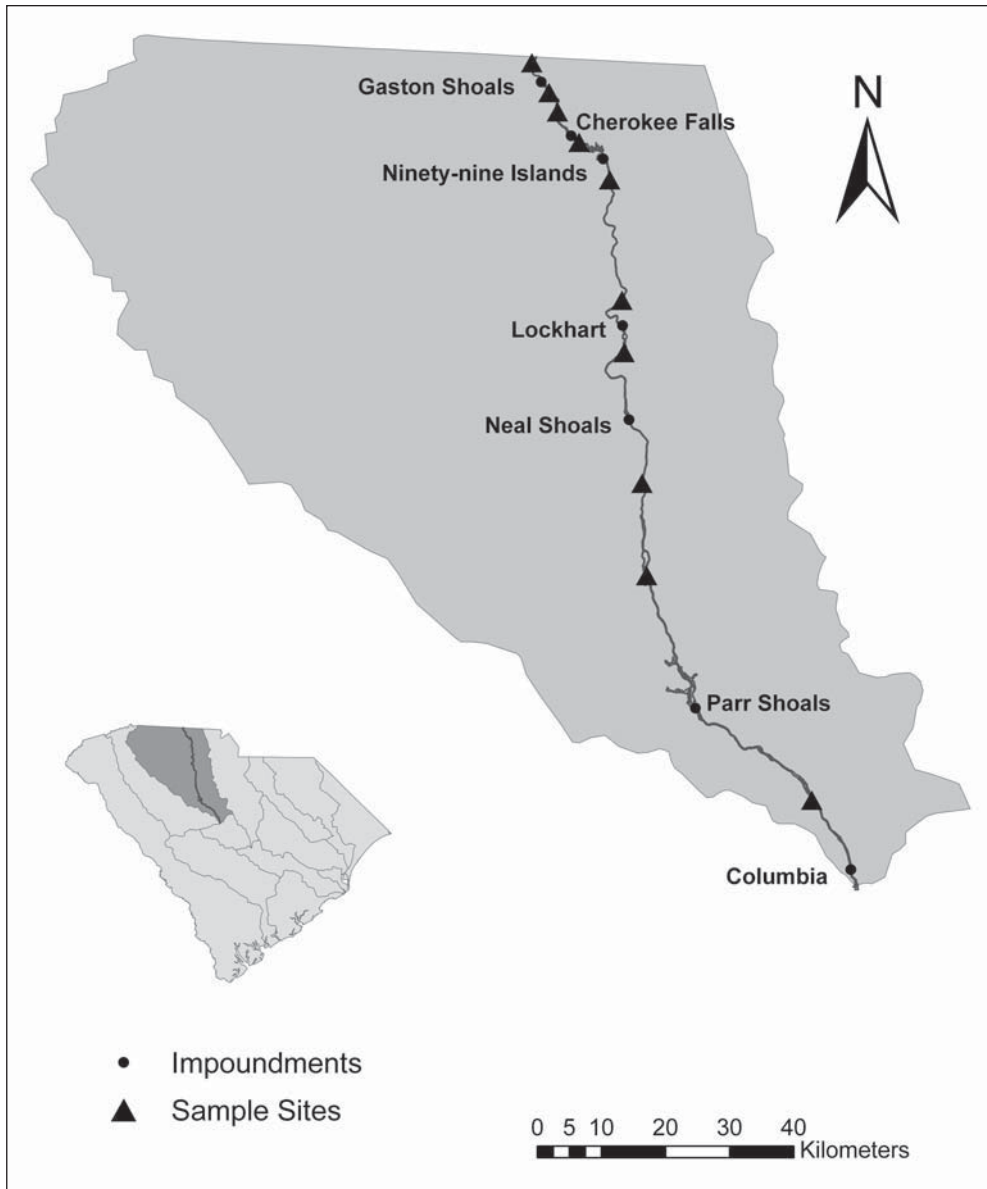


Figure 1. Broad River drainage in South Carolina, location of impoundments, and sites sampled for catostomids during 2001 and 2006–2007.

to the nearest mm TL and received an intraperitoneal or intramuscular injection of 0.5 cc of oxytetracycline (OTC, Liquamycin® LA-200®, Pfizer) to produce a chemical mark on its otoliths that could be used later to document single annulus formation per year. The fish were then transferred to the Cheraw State Fish Hatchery, SC, and placed in grow-out ponds.

During November 2002, Brassy Jumprock and Notchlip Redhorse were harvested from grow-out ponds and measured to the nearest mm TL. The lapillus otoliths were removed from each fish, cleaned of connective tissue, dried with paper towels, and placed in vials for storage. One otolith from each fish was then placed in a mold and embedded in an epoxy resin (Araldite®). A 1–2 mm-thick section was cut from the transverse plane of each embedded otolith with an Isomet® low speed saw (Buehler LTD, Lake Bluff, IL) equipped with a diamond wafering blade. Sections were mounted with an adhesive (Crystalbond™ 509, Electron Microscopy Sciences) onto numbered microscope slides, sanded with 400–1500 grit sandpaper to remove saw marks, and polished on a felt pad with a 0.3-μm polishing compound. Prepared sections were viewed at various magnifications with a compound microscope and transmitted light. Otoliths were read independently by two experienced readers, who estimated the age of each fish by counting the number of opaque bands (annuli) (Fig. 2). Disagreements were resolved by concurrence between the original readers and a third experienced reader when disputed otoliths were reread simultaneously and discussed. Age agreement could not be reached for one Brassy Jumprock and one Notchlip Redhorse. Otolith sections were examined for fluorescent OTC marks with a JenaLumar compound microscope (Zeiss Microscopy Group, Germany) equipped with a 50-W mercury arc light source, and a filter set consisting of a 475-nm excitation filter, a 505-nm dichroic mirror, and a 535-nm emission filter.

Based on the results of the OTC study, a subsequent study was initiated to determine when annulus formation occurred. Notchlip Redhorse and Brassy Jumprock were collected from one site on the lower Broad River near Columbia, SC at least once every two months from September 2006 through June 2007. Otoliths were prepared for age estimation as previously described, and marginal increment analysis was used to determine the season of annulus formation. The marginal increment ratio (MIR) was calculated as:

$$\text{MIR} = (R - R_n) / (R_n - R_{n-1}),$$

where R is the distance from the nucleus to the outer margin of the lapillus, R_n is the distance from the nucleus to the outer edge of the last opaque band, and R_{n-1} is the distance to the outer edge of the second to last complete opaque band. MIR was only calculated for fish with two or more complete annuli.

Population characteristics

Notchlip Redhorse and Brassy Jumprock were collected with boat-mounted electrofishing gear from 10 sites along the Broad River during spring (April and May) and fall (October and November) 2001 (Fig. 1). Fish were measured to the nearest mm TL and weighed to the nearest gram. Lapillus otoliths were removed during fall from up to four fish selected randomly from predetermined 25-mm

length groups, and processed for age estimation as described previously. Because we assumed fish caught in October and November had completed nearly all of their growth for the year, we counted the margin as an annulus when estimating fish age. This convention allowed for easier comparisons with growth studies that relied on back-calculated ages, or that estimated ages using spring-caught fish. Precision in age estimates between readers was assessed with the coefficient of variation (CV), estimated as:

$$CV_j = 100 \times (\sqrt{\sum_{i=1}^R [(X_{ij} - X_j)^2] / (R - 1)}) / X_j,$$

where X_{ij} is the i th estimated age of the j th fish, X_j is the mean age estimate of the j th fish, and R is the number of age estimates for each fish (Campana et al. 1995). Since not all collected fish were aged, un-aged fish within 25-mm length groups were assigned an age using a computerized age-length key (Isermann and Knight 2005) designed for that purpose. Growth of each species was estimated with a Von Bertalanffy growth equation,

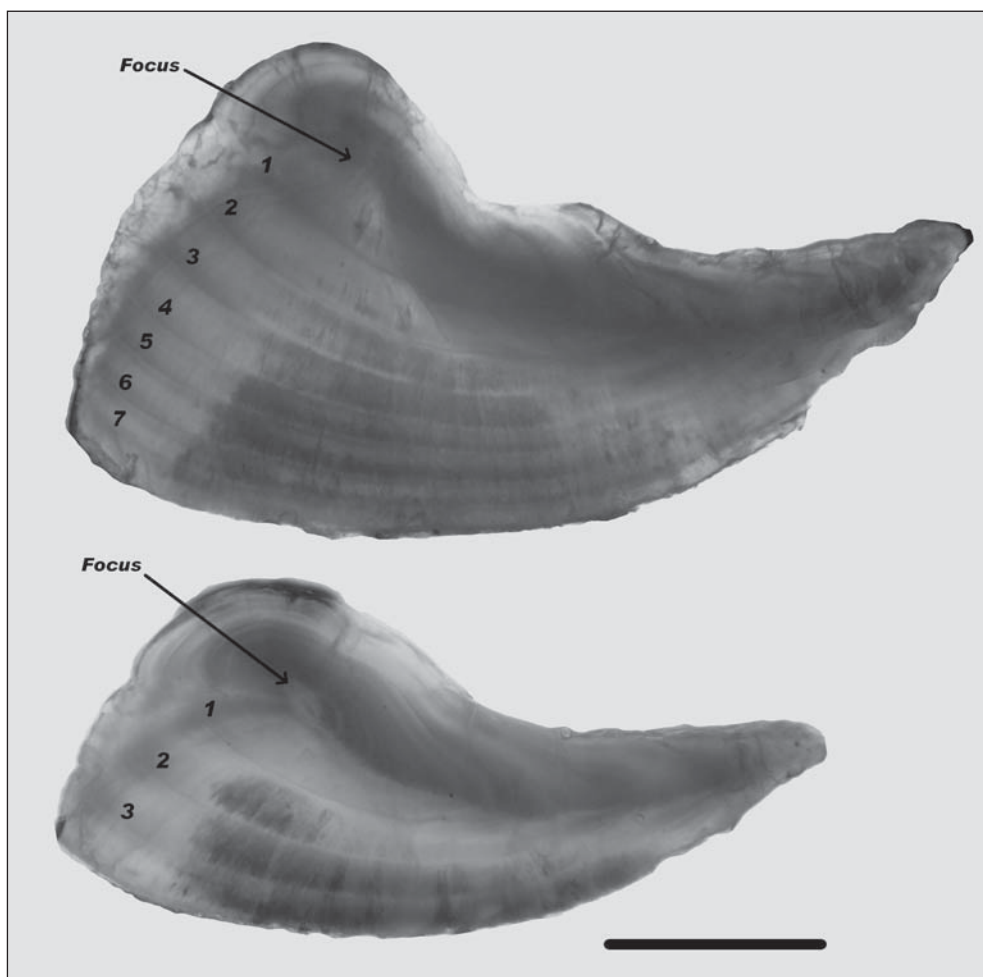


Figure 2. Sectioned lapillus otoliths from a 7-year-old (A) and 3-year-old (B) Brassy Jumprock. Scale bar = 1 mm.

$$L_t = L_\infty (1 - e^{-k(t-t_0)}),$$

where L_t = length at time t , L_∞ = asymptotic length, k = growth coefficient, and t_0 = the theoretical age where $L_t = 0$ (Von Bertalanffy 1938). Instantaneous total mortality (Z) of each species was estimated with a catch-curve based on the age frequency data for fall-caught age 3 to age 13 Notchlip Redhorse and age 3 to age 10 Brassy Jumprock (Ricker 1975). Instantaneous natural mortality was estimated with the equation suggested by Hoenig (1983),

$$M = 4.22 (T_{\max})^{-0.982},$$

where T_{\max} = maximum observed age in the population. Linear regression was used to describe the relationship between \log_{10} transformed TL and \log_{10} transformed weight for Notchlip Redhorse and Brassy Jumprock collected during spring and fall. Observations having studentized residuals with absolute values greater than 2.5 were considered outliers and were eliminated from regression analysis. Analysis of covariance (ANCOVA) was used to test for seasonal differences in regression parameters for each species.

Results

Annulus validation

On 5 November 2002, 12 Brassy Jumprock and 14 Notchlip Redhorse were harvested from ponds at the Cheraw State Fish Hatchery. Survival of Brassy Jumprock (13%) was poor, while that of Notchlip Redhorse was moderate (43%). Estimated ages of OTC-injected Brassy Jumprock and Notchlip Redhorse ranged from 3 to 13 and 4 to 13, respectively. OTC marking efficacy was 100%, with each of the 26 otoliths examined having an OTC mark on or just before the last fully formed annulus. Based on distances between earlier annuli, we determined that the space between the last annulus and the margin represented a year's growth.

One hundred forty Brassy Jumprock (mean TL = 304 mm, range = 97–447 mm) and 107 Notchlip Redhorse (mean TL = 411 mm, range = 157–567 mm) were collected for marginal increment analysis. Age was estimated for 57 Brassy Jumprock and 62 Notchlip Redhorse. Ages of Brassy Jumprock ranged from 1 to 14, and ages of Notchlip Redhorse ranged from 0 to 21. Fifty-five Brassy Jumprock and 46 Notchlip Redhorse between age 2 and age 12 were included in the marginal increment analysis. The mean marginal increment ratio increased from September through April for each species, then decreased sharply between May and June, indicating that annulus formation occurred during that period (Fig. 3).

Population characteristics

Two hundred fifteen Brassy Jumprock (mean TL = 296 mm, range = 76–424 mm) and 429 Notchlip Redhorse (mean TL = 357 mm, range = 143–518 mm) were collected from ten sites along the Broad River during 2001 (Table 1, Fig. 4). For Notchlip Redhorse and Brassy Jumprock, the spring and fall TL-Wt regression slopes were significantly different (ANCOVA, $P < 0.0001$), indicating that the two species have different trends in weight relative to length between spring

and fall. The TL-Wt relationship was significant for Notchlip Redhorse and Brassy Jumprock during both seasons ($P < 0.0001$; Table 1).

Lapilli were removed from 75 Brassy Jumprock and 121 Notchlip Redhorse and aged. Agreement between readers was 77% and 72% for Brassy Jumprock and Notchlip Redhorse, respectively. For Brassy Jumprock, reader differences ranged from 1 to 3 years, with the majority (94%) being 1 year (Fig. 5). For

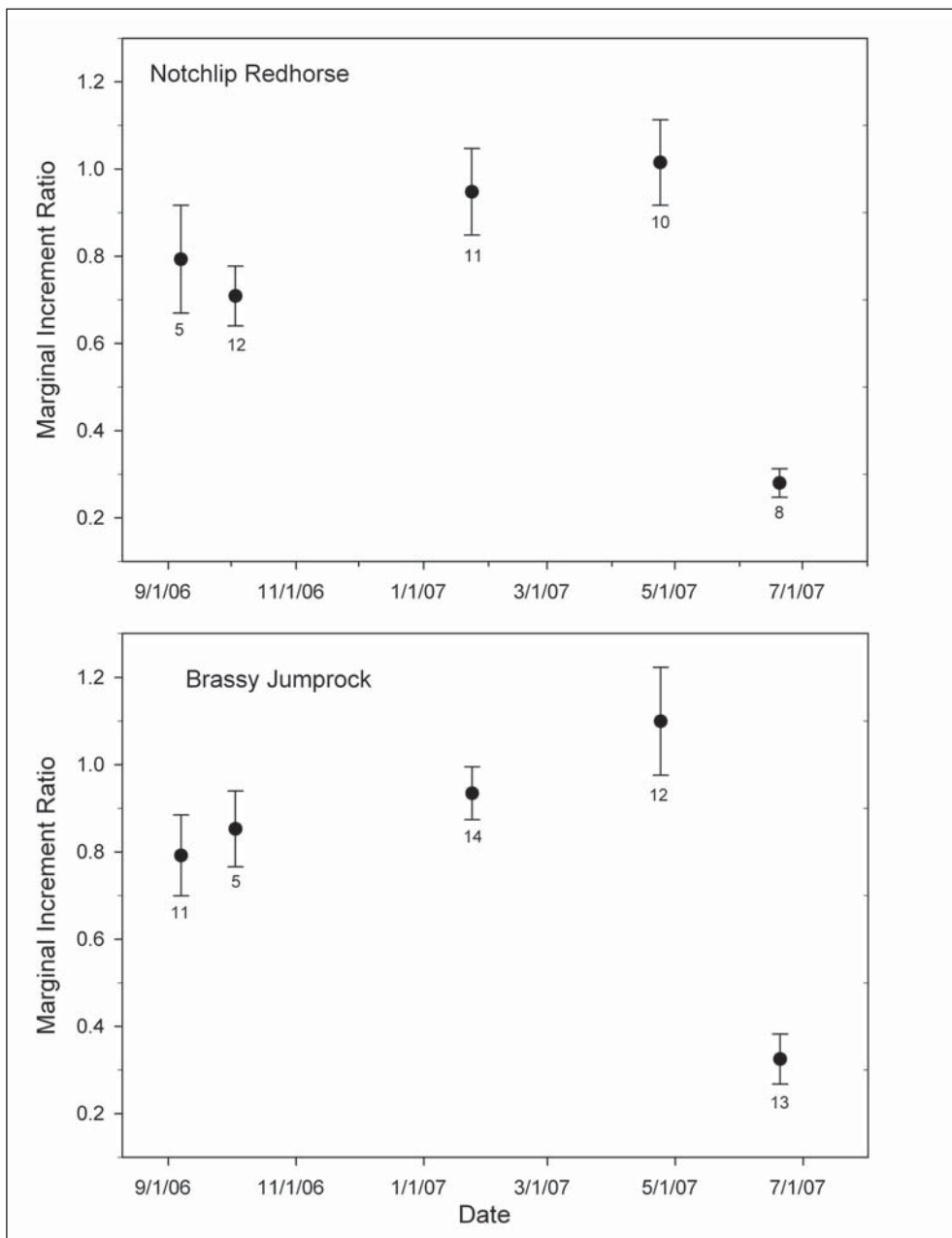


Figure 3. Mean ($\pm 2SE$) marginal increment ratio by date for Notchlip Redhorse and Brassy Jumprock collected from the Broad River near Columbia, SC during 2006 and 2007.

Notchlip Redhorse, reader differences ranged from 1 to 4 years, with the majority (86%) being 1 year (Fig. 5). Most disagreements in estimated age were due to differences identifying the first annulus. Mean CV in age estimates between readers was 5.05 for Brassy Jumprock and 4.28 for Notchlip Redhorse.

Estimated ages for Brassy Jumprock ranged from 1 to 17. For Notchlip Redhorse, they ranged from 1 to 19; an age-21 Notchlip Redhorse was collected during our marginal increment study. Plots of age-class frequency distribution (Fig. 6) indicated that both species become fully vulnerable to boat electrofishing gear in their 3rd year when they attain lengths near 300 mm TL. Age-3 fish accounted for 28% of Brassy Jumprock collected, while age-6 fish dominated Notchlip Redhorse, accounting for 37% of those fish collected. Age-4 and age-5 Notchlip Redhorse were grossly underrepresented in our samples, potentially indicating poor recruitment of those year classes and variable recruitment in general for the species. There is little if any exploitation of catostomids in the Broad River drainage, which likely contributes to their longevity.

There was large variation in length at age for Notchlip Redhorse and Brassy Jumprock (Fig. 7). Notchlip Redhorse and Brassy Jumprock grew quickly during their first four years, attaining an average length of 336 mm TL and 319 mm TL at age 4, respectively. After age 4, growth of both species slowed considerably, and neither species grew much, if at all, with regard to length beyond age 7. Von Bertalanffy growth model parameters were $L_{\infty} = 435.1$ mm TL (SE = 7.9), $t_0 = -0.12$ (SE = 0.25), and $k = 0.36$ (SE = 0.04) for Notchlip Redhorse, and $L_{\infty} = 400.3$ mm TL (SE = 8.6), $t_0 = 0.29$ (SE = 0.14), and $k = 0.43$ (SE = 0.04) for Brassy Jumprock. Estimated total instantaneous mortality Z of Notchlip Redhorse was 0.27 ($r^2 = 0.51$, $P < 0.05$); estimated instantaneous natural mortality M was 0.21. Estimated Z for Brassy Jumprock was 0.35 ($r^2 = 0.70$, $P < 0.05$); estimated M was 0.26.

Discussion

Based on our finding that one annulus is formed each year in lapillus otoliths of Notchlip Redhorse and Brassy Jumprock, we conclude that otoliths are

Table 1. Length-weight regression coefficients, standard errors in parentheses, for Brassy Jumprock and Notchlip Redhorse collected from the Broad River, SC during 2001.

Species	<i>n</i>	Mean TL		Wt (g)	Age	Slope	Intercept	<i>r</i> ²
		(mm)	TL (mm)					
Brassy Jumprock								
Spring	95	277	76–411	4–882	1–17	3.07 (0.02)	-5.12 (0.04)	0.99
Fall	112	311	103–424	9–829		3.17 (0.02)	-5.42 (0.05)	0.99
Combined	208	296	76–424	4–882		3.07 (0.01)	-5.15 (0.04)	0.99
Notchlip Redhorse								
Spring	225	351	143–518	34–1424	1–19	2.90 (0.02)	-4.73 (0.06)	0.99
Fall	190	365	157–485	45–1217		3.01 (0.02)	-5.01 (0.06)	0.99
Combined	417	357	143–518	34–1424		2.93 (0.02)	-4.81 (0.04)	0.99

appropriate structures to use for age estimation in these species. Otoliths have been shown to be reliable for estimating the ages of catostomids studied in different locales (e.g., Hutson 1999, Sylvester and Berry 2006, Quist et al. 2007). The May–June timing of annulus formation for Notchlip Redhorse and Brassy Jumprock in the Broad River agrees with that of the closely related Silver Redhorse, which forms its annulus during June–August in the Des Moines River, IA (Meyer 1962) and, at lower latitude, late April–May in the Flint River, AL

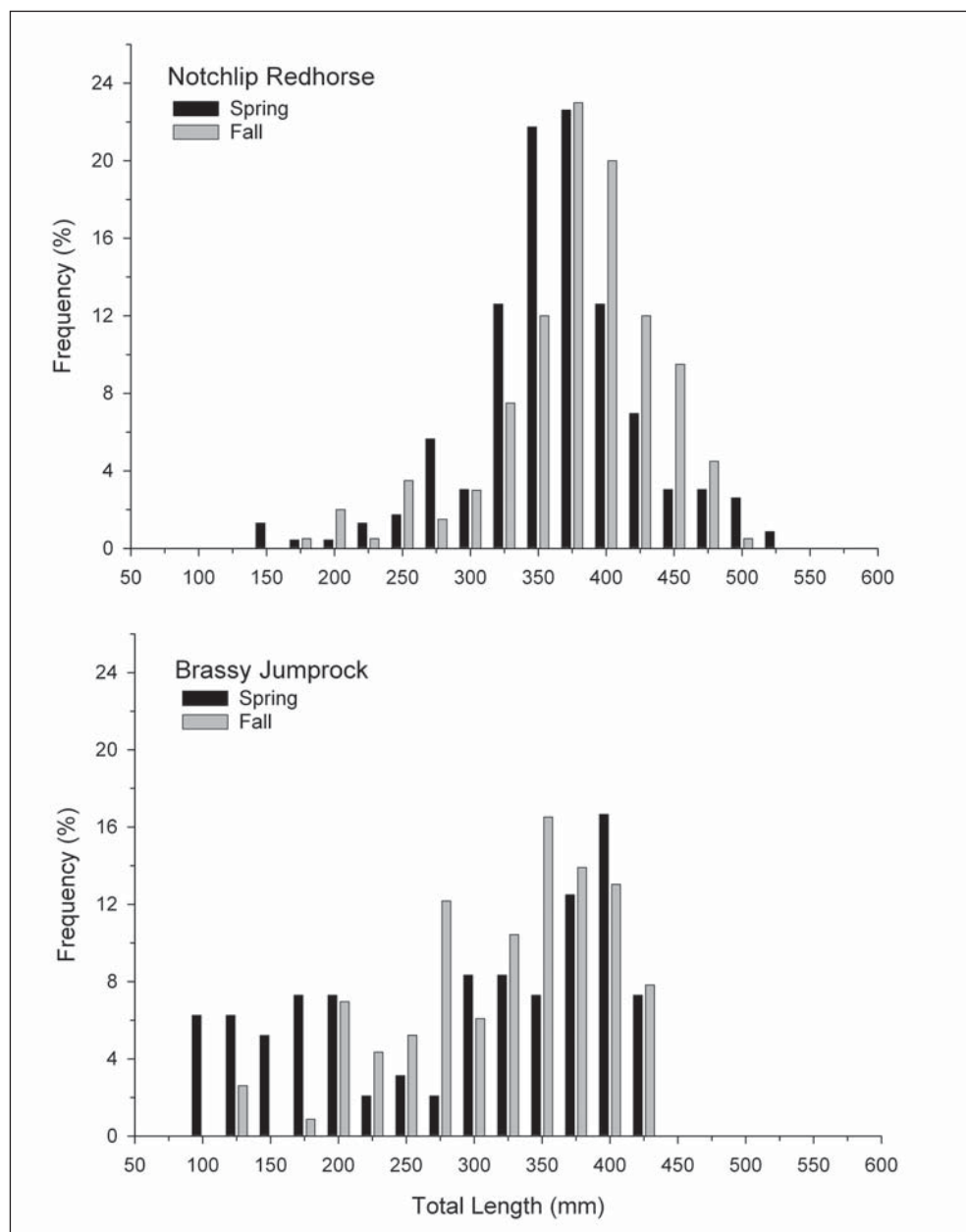


Figure 4. Length-frequency distributions for Notchlip Redhorse and Brassy Jumprock collected from the Broad River, SC during spring and fall 2001.

(Hackney et al. 1971). Other North American sucker species (Howlett 1999, Hutson 1999), and indeed, most north latitude temperate fishes (Beckman and Wilson 1995) undergo annulus formation during the same general time period in late spring.

The position of the OTC mark on or just before the last fully formed annulus was unexpected. Our initial interpretation of this result was that annulus formation occurred during fall, which would have been unusual. An alternative explanation was that the stress associated with handling, marking, and transporting the fish caused an anomalous growth check on the otoliths that was incorrectly interpreted as an annulus. However, the spacing of annuli, including the putative last annulus, on the otoliths was consistent with yearly growth. Our uncertainty lead to the marginal increment analysis that demonstrated little growth occurred

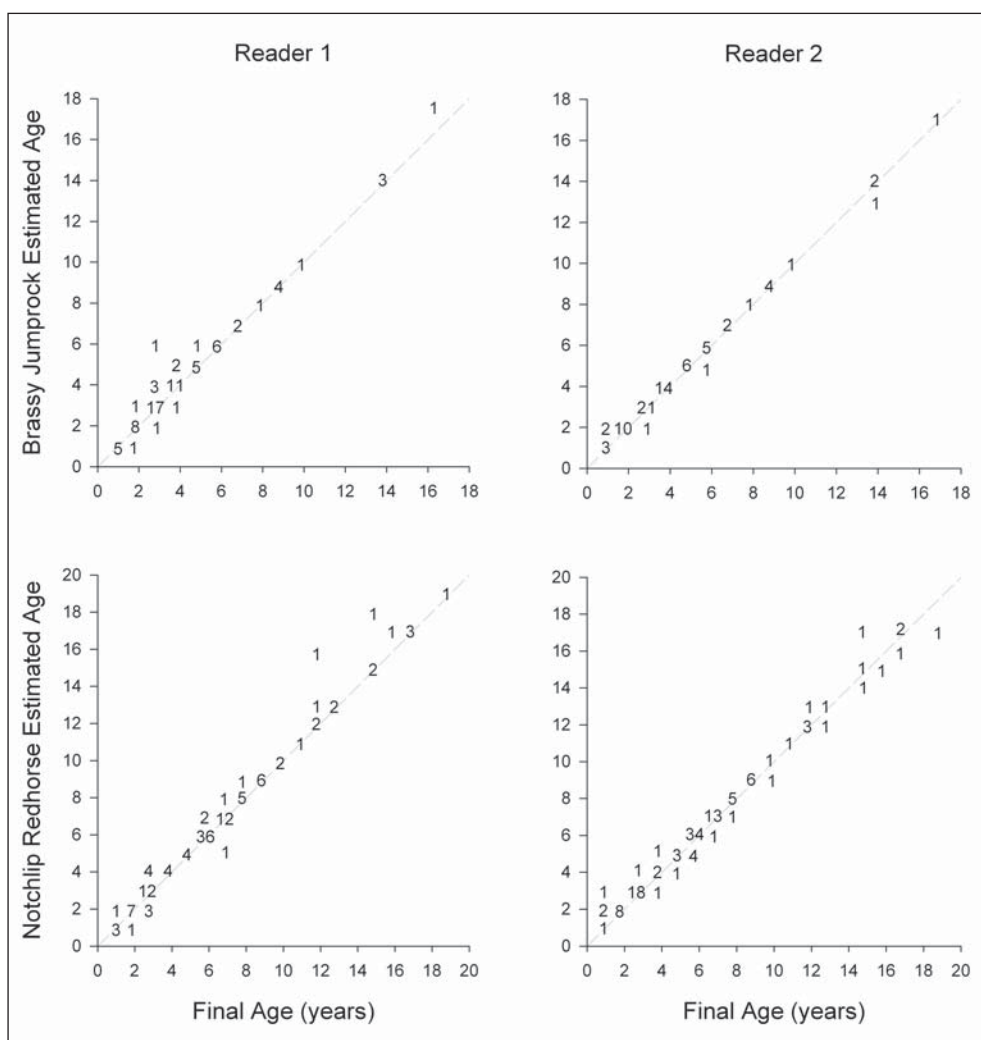


Figure 5. Age-bias graphs for two readers of Brassy Jumprock and Notchlip Redhorse otoliths. Numbers indicate sample size. Dashed line represents agreement between reader-estimated age and final estimated age as determined by a concert read.

in the otoliths of either species between November and May and that most otolith growth (roughly 70%), and presumably fish growth, occurred between July and September. Similarly, Meyer (1962) showed that most Silver Redhorse growth in the Des Moines River, IA, occurred in late July, August, and September.

In both Notchlip Redhorse and Brassy Jumprock, fish collected during spring were slightly heavier on average than fall-collected fish of similar length; however, the disparity in weight decreased with increasing length, and in Notchlip Redhorse, fall-collected fish larger than 350 mm TL were heavier than spring-collected fish of similar size. The seasonal disparity in weight for fish greater than 250 mm TL was <4% and <13% for Notchlip Redhorse

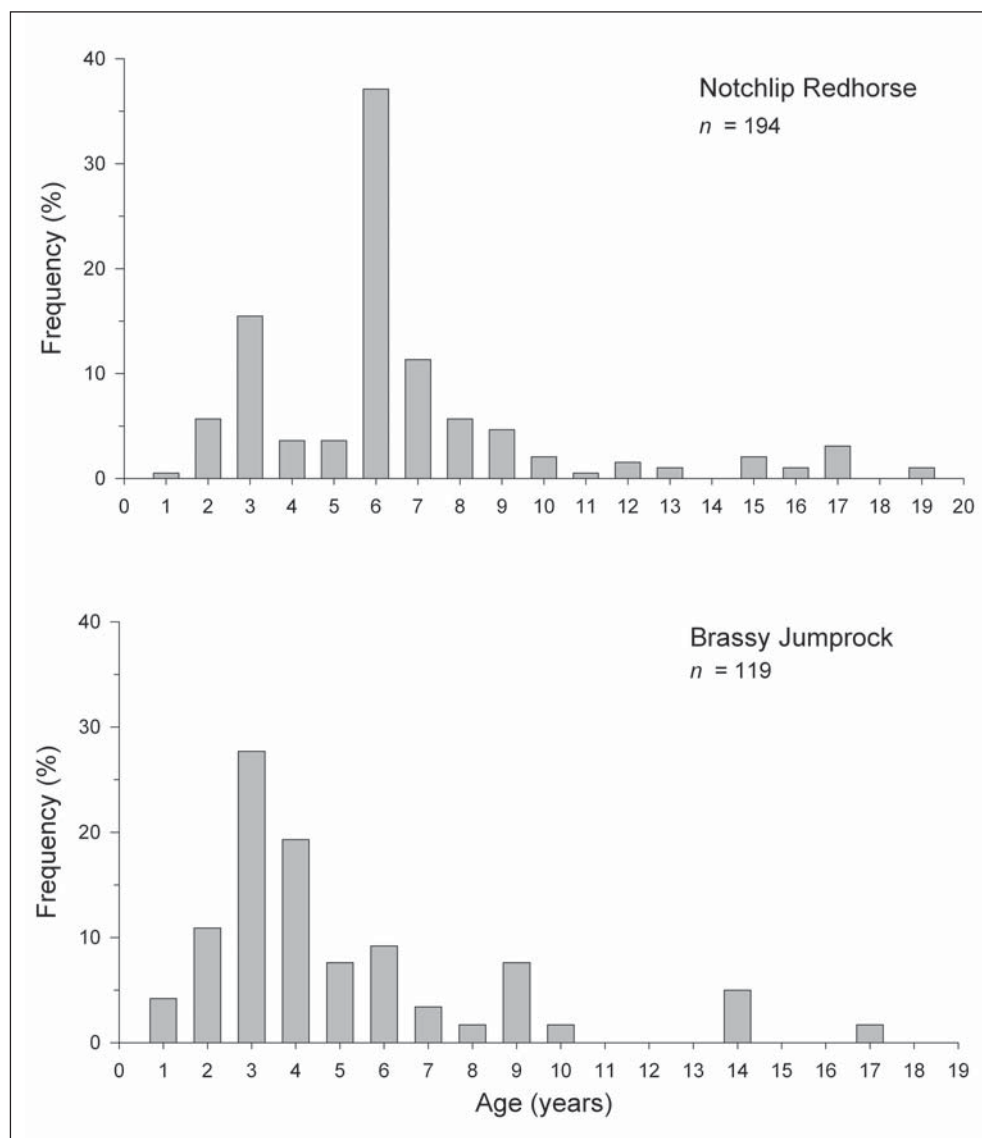


Figure 6. Age-class frequency distributions of Notchlip Redhorse and Brassy Jumprock collected from the Broad River, SC during fall 2001.

and Brassy Jumrock, respectively. Whether the differences in weight relative to length are of biological significance or the result of sampling error is unknown; it is suggested that the combined equation be used to estimate weight from length in these species.

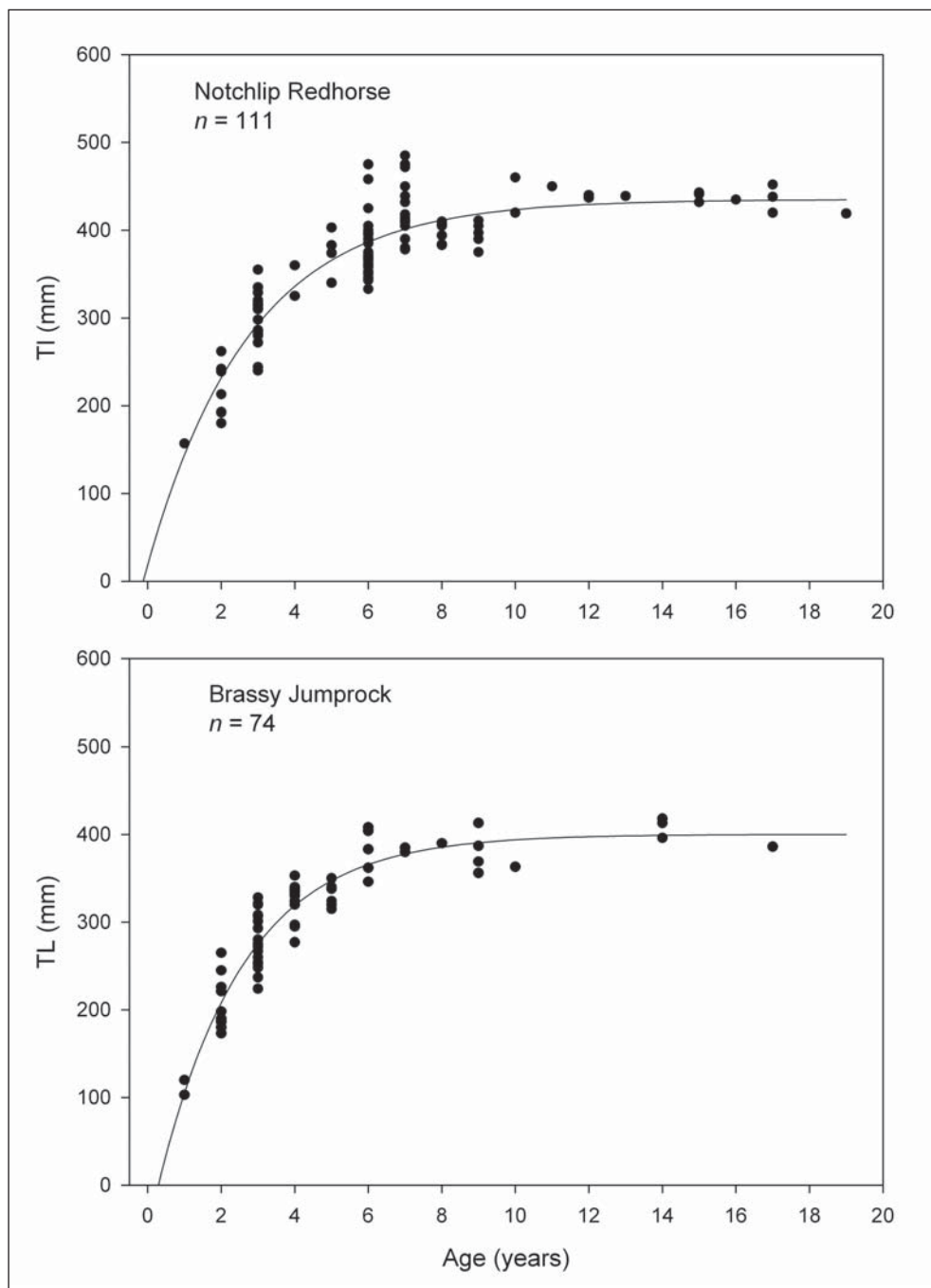


Figure 7. Von Bertalanffy growth curves based on otolith-estimated age of Notchlip Redhorse and Brassy Jumrock collected from the Broad River, SC during fall 2001.

Notchlip Redhorse and Brassy Jumprock are long-lived in the Broad River, SC. Notchlip Redhorse in the Broad River attained considerably older ages than those reported in the Savannah River, SC–GA (Grabowski et al. 2007) or for the closely related Silver Redhorse in the Flint River, AL (Hackney et al. 1971) and the Des Moines River, IA (Meyer 1962), where the oldest captured fish were age 10 or less. However, those studies used only scales to estimate age; scales have been shown to underestimate the age of older catostomids (Beamish and Harvey 1969, Quist et al. 2007, Sylvester and Berry 2006) as well as other species. Reid (2009), using fin ray sections, estimated the maximum ages of Black Redhorse and *Moxostoma macrolepidotum* Lesueur (Shorthead Redhorse) in Ontario to be 17, comparable to our maximum estimated ages for Notchlip Redhorse and Brassy Jumprock.

The diminished growth in length of Notchlip Redhorse and Brassy Jumprock after age 4 was likely due to maturation. Growth in fish length is typically fastest before maturation. Once fish reach maturity, more energy is invested in gonadal tissues than somatic tissues, which likely explains the reduced growth in both species after age 4. The closely related Silver Redhorse, as well as other moderate- and large-sized catostomids, are known to spawn by age-5 (Jenkins and Burkhead 1994). Although growth in length of both species slowed considerably after age 4, mature catostomids are heavier per unit length than immature fish, and relatively small increases in length can result in large increases in weight.

The large variation in length at age for Notchlip Redhorse and Brassy Jumprock in the Broad River could be due to several factors. First, the fish were collected from sections of river that span over 170 km, where average flows and water temperatures vary considerably from the uppermost to the lowermost sampling sites. Based on limited available data, mean annual water temperatures in the uppermost portion of the river average roughly 17 °C, while those in the lower river, below Parr Shoals Reservoir, average roughly 19 °C. Additionally, based on average annual discharge, the river at the lowermost sample site is roughly 2.5 times the size of the river at our uppermost sample site. It is possible that growth varied among sites, but limited samples from each site precluded meaningful statistical comparisons. Second, we did not determine the sex of the fish we collected, so we could not account for the possible influence of sex on the growth rates of either species. Although there was no apparent difference in growth between male and female Notchlip Redhorse in the Savannah River (Grabowski et al. 2007), older female Silver Redhorse appeared to grow faster than males in the Flint River, AL (Hackney et al. 1971), and other catostomids have been found to have differential growth based on sex (Grabowski et al. 2007).

Growth of Notchlip Redhorse in the Broad River was slower than that reported in the Savannah River (Grabowski et al. 2007). For example, an age-4 Notchlip Redhorse in the Savannah River averaged 399 mm TL, compared to 336 mm in the Broad River. Because Notchlip Redhorse from the Savannah River were aged with scales, and scales typically underestimate the ages of older fish, the slower

growth could be explained by the choice of aging structure. However, for fish less than age 5, scale ages typically have high agreement with otolith ages (e.g., Quist et al. 2007); since fish less than age 5 in the Savannah River grew faster than those in the Broad River, it is likely that growth differences for Notchlip Redhorse between the two rivers were real, at least for younger fish. Length ranges of Brassy Jumprock observed in the Broad River, SC were similar to those reported from Lake Norman, NC (Jenkins and Burkhead 1994), the only other published length information we found for Brassy Jumprock.

Mortality rates of Brassy Jumprock and Notchlip Redhorse in the Broad River were very low. There was qualitative agreement between the catch-curve derived estimates and estimates of natural mortality using the equation of Hoenig (1983). The low mortality rates suggest there is very little exploitation of either species in the Broad River, SC. Mortality estimates for Notchlip Redhorse in the Broad River were much lower than in the Savannah River, where Z was between 0.51 and 0.85; however, those high mortality estimates may have resulted in part from underestimating the age of older fish due to scale-estimated ages (Grabowski et al. 2007). Mortality estimates for Black Redhorse ($Z = 0.26$) and Shorthead Redhorse ($Z = 0.24$), other moderate-sized catostomids, in Ontario (Reid 2009) were comparable to those we observed in the Broad River.

Populations of Notchlip Redhorse and Brassy Jumprock in the Broad River, SC, appear to be secure and relatively stable, as evidenced by their high relative abundance and long life spans. Notchlip Redhorse was able to overcome the potentially detrimental effects of two consecutive poor year classes—aided, perhaps, by the particularly strong year class that preceded them. Apparently, both Notchlip Redhorse and Brassy Jumprock have been generally tolerant of a wide spectrum of human activities that are known to adversely affect more sensitive species. On the Broad River, these activities include dam construction and operation, riparian agriculture and forestry, in-stream sand mining, wastewater discharges, and creeping urbanization. The population characteristics of Notchlip Redhorse and Brassy Jumprock presented in this study are important tools for the development of management strategies in other locales where these populations may be negatively impacted by high exploitation and/or habitat degradation.

Acknowledgments

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Literature Cited

- Beamish, R.J., and H.H. Harvey. 1969. Age determination in the White Sucker. *Journal of the Fisheries Research Board of Canada* 26:633–638.
- Beckman, D.W., and C.A. Wilson. 1995. Seasonal timing of opaque zone formation in fish otoliths. Pp. 27–44, *In* D.H. Secor, J.M. Dean, and S.E. Campana (Eds.). *Recent Developments in Fish Otolith Research*. University of South Carolina Press, Columbia, SC. 735 pp.
- Bettinger, J.M., J.S. Crane, and J.S. Bulak. 2003. Broad River Aquatic Resources Inventory Completion Report. South Carolina Department of Natural Resources, Columbia, SC.
- Campana, S.E., M.C. Annand, and J.I. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society* 124:131–138.
- Cooke, S.J., C.M. Bunt, S.J. Hamilton, C.A. Jennings, M.P. Pearson, M.S. Cooperman, and D.F. Markle. 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. *Biological Conservation* 121:317–331.
- Curry, K.D., and A. Spacie. 1984. Differential use of stream habitat by spawning catostomids. *American Midland Naturalist* 111:267–279.
- Grabowski, T.B., N.L. Ratterman, and J.J. Isely. 2007. Demographics of the spawning aggregations of four castostomid species in the Savannah River, South Carolina and Georgia, USA. *Ecology of Freshwater Fish* 17:318–327.
- Hackney, P.A., G.R. Hooper, and J.F. Webb. 1971. Spawning behavior, age and growth, and sport fishery for the Silver Redhorse, *Moxostoma anisurum* (Rafinesque), in the Flint River, Alabama. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* 24(1970):569–576.
- Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* 82:898–903.
- Hoff, G.R., D.J. Logan, and D.F. Markle. 1997. Otolith morphology and increment validation in young Lost River and Shortnose Suckers. *Transactions of the American Fisheries Society* 126:488–494.
- Howlett, D. 1999. Age, growth, and population structure of Black Redhorse (*Moxostoma duquesnei*) and Golden Redhorse (*Moxostoma erythrurum*) in Southwest Missouri. M.Sc. Thesis. Southwest Missouri State University, Springfield, MO. 58 pp.
- Hutson, C.A. 1999. Aging validation, growth, and comparison of four age estimators of the River Redhorse (*Moxostoma carinatum*). M.Sc. Thesis. Southwest Missouri State University, Springfield, MO. 37 pp.
- Isermann, D.A., and C.T. Knight. 2005. A computer program for age-length keys incorporating age assignment to individual fish. *North American Journal of Fisheries Management* 25:1153–1160.
- Jenkins, R.E., and N.M. Burkhead. 1994. *Freshwater Fishes of Virginia*. American Fisheries Society. Bethesda, MD. 1080 pp.
- Lee, D.S., C.R. Gilbert, C.H. Hocutt, R.E. Jenkins, D.E. McAllister, and J.R. Stauffer, Jr. (Eds.). 1980. *Atlas of North American Freshwater Fishes*. North Carolina State Museum of Natural History, Raleigh, NC. 867 pp.
- Meyer, W.H. 1962. Life history of three species of redhorse (*Moxostoma*) in the Des Moines River, Iowa. *Transactions of the American Fisheries Society* 91:412–419.

- Nelson, J.S., E.J. Crossman, H. Espinosa-Pérez, L.T. Findley, C.R. Gilbert, R.N. Lea, and J.D. Williams. 2004. Common and Scientific Names of Fishes from the United States, Canada, and Mexico. American Fisheries Society, Special Publication 29, Bethesda, MD. 386 pp.
- Quist, M.C., Z.J. Jackson, M.R. Bower, and W.A. Hubert. 2007. Precision of hard structures used to estimate age of riverine catostomids and cyprinids in the upper Colorado River Basin. *North American Journal of Fisheries Management* 27:643–649.
- Reid, S.M. 2009. Age, growth, and mortality of Black Redhorse (*Moxostoma duquesnei*) and Shorthead Redhorse (*M. macrolepidotum*) in the Grand River, Ontario. *Journal of Applied Ichthyology* 25:178–183.
- Ricker W. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* 191:382.
- Sylvester R.M., and C.R. Berry, Jr. 2006. Comparison of White Sucker age estimates from sales, pectoral fin rays, and otoliths. *North American Journal of Fisheries Management* 26:24–31.
- Thompson, K.R., and D.W. Beckman. 1995. Validation of age estimates from White Sucker otoliths. *Transactions of the American Fisheries Society* 124:637–639.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Human Biology* 10:181–213.