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Demographics of the spawning aggregations of four catostomid species in the Savannah River, South Carolina and Georgia, USA

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Abstract – Differences in the life history strategies employed by otherwise ecologically similar species of a fish assemblage may be an important factor in the coexistence of these species and is an essential consideration in the conservation and management of these assemblages. We collected scales to determine age and growth of four species of the catostomid assemblage (northern hogsucker *Hypentelium nigricans*, spotted sucker *Minytrema melanops*, notchlip redhorse *Moxostoma collapsum* and robust redhorse *Moxostoma robustum*) of the Savannah River, Georgia–South Carolina in spring 2004 and 2005. Robust redhorse was the largest species; reaching sexual maturity at an older age and growing faster as a juvenile than the other species. Spotted sucker did not achieve the same size as robust redhorse, but reached sexual maturity at younger ages. Notchlip redhorse was intermediate between the abovementioned two species in age at maturity and size. Northern hogsucker was the smallest species of the assemblage and reached the sexual maturity at the age of three. Both robust redhorse and spotted sucker were sexually dimorphic in size-at-age. The range of life history strategies employed by Savannah River catostomids encompasses the range of life history strategies exhibited within the family as a whole.

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Key words: Catostomidae; age and growth; spawning aggregations; Savannah River

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Introduction

Fishes in the family Catostomidae demonstrate a wide range of life history strategies (Beamish 1973; Cooke et al. 2005). Studies suggest smaller-bodied suckers such as chubsuckers *Erimyzon* spp. (Wagner & Cooper 1963; Jenkins & Burkhead 1993) and torrent suckers *Thoburnia* spp. (Raney & Lachner 1946b; Jenkins & Burkhead 1993) are short-lived fast-growing species, while larger bodied catostomids tend to fall into one of two general categories. Some of these larger species are long-lived (>20 years) and relatively slow growing, such as blue suckers *Cycleptus* spp. (Peterson et al. 1999; Vokoun et al. 2003), many of the western suckers *Catostomus* spp. and *Chasmistes* spp. (Scoppettone 1988), and possibly some redhorses *Moxostoma* spp. (Jenkins & Burkhead 1993). The remaining species, such as carpsuckers *Carpiodes* spp. (Woodward & Wissing 1976), hogsuckers *Hypentelium* spp. (Raney & Lachner 1946a) and redhorses (Meyer 1962; Bowman 1970; Hackney et al. 1971; Jenkins & Burkhead 1993), seem to exhibit intermediate life-spans (8–16 years) and growth rates. These three general life history strategies would generally seem to fall into the opportunistic, equilibrium and periodic strategies proposed by Winemiller & Rose (1992), although the lack of data regarding other aspects of catostomid biology such as interspecific differences in fecundity or parental investment per individual progeny means this framework should be applied cautiously. These life history traits also

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demonstrate the potential for a high degree of plasticity among populations within a species (Beamish 1973; Duchesne & Magnan 1997). However, there is a paucity of life history data available in the literature for interpopulation comparisons or even for examining differences in age and growth among species within a river system.

The Savannah River offers an opportunity to examine a diverse assemblage of catostomids. Seven species inhabit the main channel of the river, including northern hogsucker *Hypentelium nigricans* (Lesueur), spotted sucker *Minytrema melanops* (Rafinesque), quillback *Carpiodes cyprinus* (Lesueur), highfin carpsucker *Carpiodes velifer* (Rafinesque), notchlip redhorse *Moxostoma collapsum* (Cope), the imperiled robust redhorse *Moxostoma robustum* (Cope) and the undescribed brassy jumprock *Moxostoma* sp. (Marcy et al. 2005). Of these species, limited demographic data are available for northern hogsucker (Raney & Lachner 1946a; Carlander 1969), spotted sucker (Carlander 1969; Pflieger 1975), quillback and highfin carpsucker (Carlander 1969; Woodward & Wissing 1976). The notchlip redhorse was formerly considered an Atlantic Slope subspecies of silver redhorse *Moxostoma anisurum* (Rafinesque) and has only recently been elevated to species status (Warren et al. 2000; Nelson et al. 2004). Although several age and growth studies have been published for silver redhorse (Meyer 1962; Carlander 1969; Hackney et al. 1971), none have been conducted for populations of what are now considered notchlip redhorse. Likewise, there are no published reports of age and growth available for robust redhorse or brassy jumprock.

The lack of basic life history and demographic data available for some riverine catostomids may be partially a reflection of difficulties capturing sufficient numbers of these fishes in large rivers (Cooke et al. 2005; Grabowski & Isely 2006). However, catostomids tend to form spawning aggregations in shallow water where they are vulnerable to various sampling gears (Jenkins & Burkhead 1993; Grabowski & Isely 2005, 2007a). As part of an ongoing study, we were able to collect data from a large number of catostomids captured from their spawning habitat. Our objectives were to evaluate the size and age structure, growth, and mortality of the catostomid populations comprising these spawning aggregations in the main channel of the lower Savannah River.

Methods

Study area

We captured catostomids in the lower Savannah River below New Savannah Bluff Lock and Dam (NSBLD) in Augusta, Georgia, between river kilometres (rkm) 300 and 280. Our efforts were focused on the two mid-channel gravel bars that occur within this reach. These structures are unique in the lower Savannah River and have been identified as important spawning habitat for catostomids (Grabowski & Isely 2006, 2007a). The upstream gravel bar is located at rkm 299.4 immediately below the tailrace of NSBLD. This structure encompasses an area of approximately 25,500 m^2 and consists of a thin layer of gravel mixed with sand. The upstream gravel bar attracts spawning aggregations of carpsuckers, spotted sucker, notchlip redhorse and robust redhorse (Grabowski & Isely 2007a). The lower gravel bar is approximately 16 rkm downstream of NSBLD and is only about 4200 m^2 in area. The lower gravel bar is composed of a relatively thick layer of coarse gravel over sand and appears to be used as spawning substrate only by robust redhorse (Grabowski & Isely 2007a).

Fish collection

Sampling was conducted on the main channel gravel bars during the spring of 2004 (1 April–1 June) and 2005 (14 March–1 June) using prepositioned grid electrofishers (Grabowski & Isely 2005, 2007a). Boat electrofishing in adjacent deep water-holding areas was used to supplement collections made on the gravel bars. Captured suckers were measured: to the nearest mm total length (mm TL), weighed (g) and photographed. The sex of each individual was determined based upon the expression of gametes and secondary sex characteristics (presence of nuptial tubercles in males, loss of mucus in females) in reproductively active individuals and by the shape of the pelvic fins in individuals not reproductively active (Jenkins & Burkhead 1993). Three to five scales were removed from an area posterior to the pectoral fin, immediately below the lateral line. All fish were released alive.

Scale microstructure analysis

Scales were prepared and interpreted following the protocols of Van Oosten (1929), and Devries & Frie (1996). Briefly, we examined acetate impressions of scales projected at 24X magnification onto frosted glass. We measured the scale radius from the focus to each annulus and to the margin. Each scale was examined by two independent readers. Discrepancies were resolved by a third reader.

Total length at age was back calculated for each annulus and corrected using the Fraser–Lee method (Fraser 1916; Lee 1920). Based upon previous collections (Grabowski, unpublished data), data from captive rearing programs (F. Sessions, South Carolina Department of Natural Resources, personal communication), and a review of the available literature (Meyer

1962; Hackney et al. 1971; Hogue & Buchanan 1977; White 1977; Fuiman 1979; Fuiman & Witman 1979; Kay et al. 1994), 30 mm TL was used as the estimated size at scale formation for all species.

Data analysis

We used analysis of covariance (ANCOVA) to assess differences in growth between males and females within species. A von Bertalanffy growth curve, $L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right)$ where L_t = length at time t, L_∞ = asymptotic length, K is a growth coefficient and t_0 is a time coefficient where length would theoretically be zero (Von Bertalanffy 1938), was developed from back-calculated length-at-age data for each species, and fitted to males and females within a species where appropriate. Back calculated total lengths at age were used to provide some estimate of early growth for fitting the Von Bertalanffy growth curve. However, it should be noted that the growth curves generated using this data present conservative estimates of early growth because back calculated lengths at age are likely to underestimate growth because of scale resorption. Instantaneous mortality (Z) for each species was estimated from the slope of the descending leg of a catch curve and converted to annual mortality (A) as described by Ricker (1975). Interspecific comparisons of Z were made using ANCOVA. All means and parameter estimates are presented ± SE. A significance level of $\alpha = 0.05$ was used for all statistical comparisons.

Results

A total of 238 suckers was collected in spring of 2004: two brassy jumprocks (one male; one female), 30 northern hogsuckers (22 males; eight females), 63 spotted suckers (30 males; 33 females), 91 notchlip redhorse (75 males; 16 females) and 52 robust redhorse (39 males; 13 females). In spring of 2005, 102 suckers were captured: a single male quillback, seven northern hogsuckers (four males; three females), eight notchlip redhorse (seven males; one female) and 86 robust redhorse (70 males; 16 females). An additional 16 robust redhorse (11 males; five females) were captured in 2002–2003 from the same locations and were included in age and growth analyses. No adult highfin carpsuckers were captured. Consequently, brassy jumprock, quillback and highfin carpsucker were excluded from further analysis because of low sample sizes.

All captured individuals were adult fish exhibiting characteristics of reproductive condition such as full development of nuptial tubercles, loss of body mucus and expression of gametes. Northern hogsuckers were the exception, as the majority of individuals exhibited no external signs of reproductive activity. Individuals of each species exhibited length frequency distributions different from that of other species ($\chi^2 \geq 40.13$, d.f. ≥ 10, $P < 0.0001$). As shown in Fig. 1, robust redhorse was the largest species encountered on the gravel bars ($F = 2658.6$, d.f. = 1, 349 and $P < 0.0001$) while northern hogsucker was consistently the smallest ($F = 1454.3$, d.f. = 1, 349 and $P < 0.0001$). Notchlip redhorse and spotted sucker did not exhibit any differences in mean total length ($F = 0.07$, d.f. = 1, 349 and $P = 0.79$). Female robust redhorse ($t = 5.59$, d.f. = 152 and $P < 0.0001$) and spotted sucker ($t = 2.33$, d.f. = 61 and $P = 0.02$) comprised a higher proportion of larger individuals. No difference in size between sexes was detected in other species ($t \leq -0.31$, $P \geq 0.14$). Estimates of Z ranged from 0.508 for robust redhorse to 0.852 for spotted sucker; however, no difference in instanta-

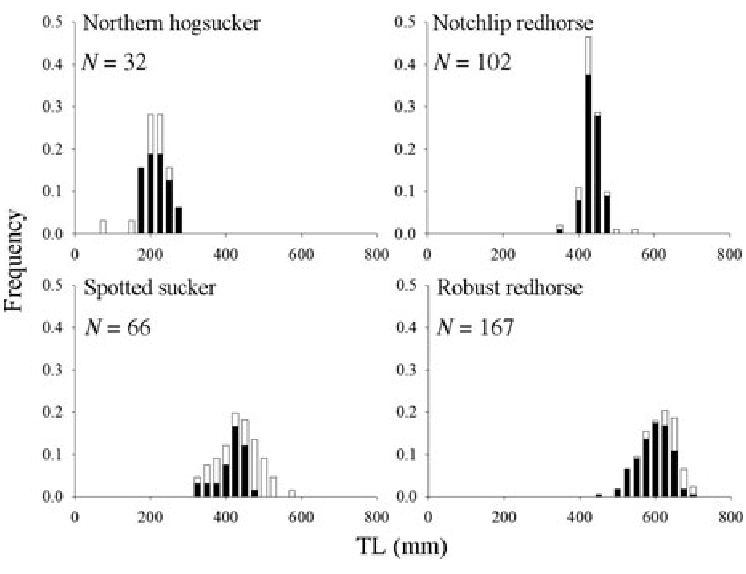

Fig. 1. Length frequency distributions of male (black bars) and female (white bars) of northern hogsucker, spotted sucker, notchlip redhorse and robust redhorse captured in the Savannah River, South Carolina–Georgia in spring 2004 and 2005.

Table 1. Mean (±SE) back-calculated total length (TL) at each annulus of northern hogsucker from the Savannah River, South Carolina–Georgia.

			TL (mm) at capture		Back calculated TL (mm) at age				
Age group	Year class	*N*	Mean	Range	1	2	3	4	5
0	–	–	–	–					
I	2004	5	102.0 ± 12.9	70–136	92.0 ± 8.0				
II	2002, 2003	4	186.8 ± 9.8	153–214	100.1 ± 8.7	177.8 ± 9.9			
III	2001, 2002	13	203.0 ± 3.0	175–214	88.0 ± 2.1	155.0 ± 3.9	203.0 ± 5.4		
IV	2000, 2001	13	227.6 ± 4.6	200–249	79.3 ± 1.9	139.8 ± 3.5	193.2 ± 4.3	227.6 ± 4.6	
V	1999	3	265.3 ± 8.2	249–274	80.0 ± 2.8	137.9 ± 1.0	190.6 ± 6.5	230.8 ± 4.7	265.33 ± 8.2
Mean TL (mm) at age					86.2 ± 1.9	150.2 ± 3.2	197.3 ± 3.2	228.2 ± 3.8	265.3 ± 8.2
Mean annual growth (mm)					86.2 ± 1.9	64.9 ± 1.9	50.9 ± 2.6	35.5 ± 2.0	34.5 ± 4.3

neous mortality rates (F = 0.75, d.f. = 7, 19 and P = 0.89) between Savannah River catostomids was detected.

Over 80% of captured northern hogsuckers were three (N = 13) or four (N = 13) years old but individuals ranged from age one to five. Back calculated total lengths for northern hogsuckers in the Savannah River indicate that individuals grow rapidly during their first 3 years reaching 197.3 ± 3.2 mm TL before experiencing a decrease in annual growth in subsequent years (Table 1). No sex effect on the age-length relationship (F = 0.31, d.f. = 1, 110 and P = 0.58) was detected. Therefore, a von Bertalanffy growth curve was fitted for both sexes combined. This yielded a model with parameters of L_∞ = 329.7 ± 25.3, k = 0.332 ± 0.049 and t_0 = 0.373 ± 0.063 (Fig. 2).

Approximately 80% of captured spotted suckers were 3–4 years old but individuals as old as eight were encountered (Tables 2 and 3). Both sexes grew rapidly until age 3−4. However, females were larger than males at a given age (F = 6443.9, d.f. = 2, 416 and

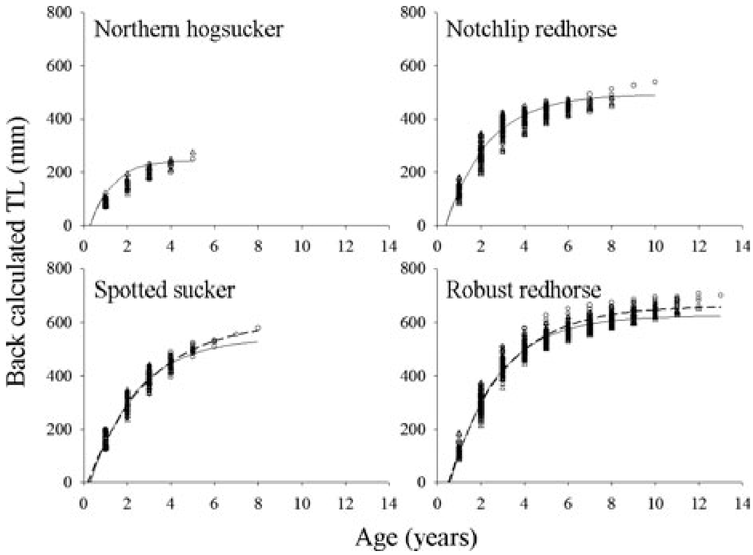

Fig. 2. Von Bertalanffy growth curves based on back calculated total length at age of northern hogsucker, spotted sucker, notchlip redhorse and robust redhorse captured in the Savannah River, South Carolina–Georgia in spring 2004 and 2005. Males are represented by open triangles while open circles denote females. Solid lines represent growth curves fitted to males, while dashed lines indicate female growth curves.

Table 2. Mean (±SE) back-calculated total length (TL) at each annulus of male spotted sucker from the Savannah River, South Carolina–Georgia.

			TL (mm) at capture		Back calculated TL (mm) at age					
Age group	Year class	*N*	Mean	Range	1	2	3	4	5	6
0	–	0	–	–						
I	–	0	–	–						
II	2002	1	318	–	164.5	318				
III	2001	9	380.8 ± 9.0	336–418	155.7 ± 8.1	288.9 ± 9.5	380.8 ± 9.0			
IV	2000	19	438.1 ± 3.9	413–474	152.1 ± 5.0	300.8 ± 6.4	402.9 ± 5.2	438.1 ± 3.9		
V	–	0	–	–						
VI	1998	1	529	–	137.5	260.3	395.9	467.6	500.9	529
Mean TL (mm) at age					153.1 ± 4.0	296.4 ± 5.2	395.8	439.6 ± 4.0	500.9	529
Mean annual growth (mm)					153.1 ± 4.0	139.5 ± 5.9	97.4 ± 4.6	34.0 ± 4.1	33.3	28.1

Table 3. Mean (±SE) back-calculated total length (TL) at each annulus of female spotted sucker from the Savannah River, South Carolina–Georgia.

Age group	Year class	*N*	TL (mm) at capture		Back calculated TL (mm) at age							
			Mean	Range	1	2	3	4	5	6	7	8
0	–	0	–	–								
I	–	0	–	–								
II	–	0	–	–								
III	2001	8	374.8 ± 11.0	335–437	156.2 ± 10.4	274.8 ± 12.2	374.8 ± 11.0					
IV	2000	14	447.2 ± 7.5	395–490	156.0 ± 7.6	292.1 ± 8.2	401.2 ± 7.2	447.2 ± 7.5				
V	1999	8	497.8 ± 6.0	470–526	146.7 ± 4.0	284.8 ± 7.0	385.0 ± 13.1	458.9 ± 7.7	497.8 ± 6.0			
VI	1998	2	520.0 ± 10.0	510–530	135.5 ± 2.3	286.1 ± 24.3	366.4 ± 24.6	438.8 ± 10.9	498.8 ± 7.3	520.0 ± 10.0		
VII	1997	0	–	–	–	–	–	–	–	–	–	
VIII	1996	1	580	–	170.4	334.3	430.2	474.7	516.8	535.5	556.6	580
Mean TL (mm) at age					152.9 ± 4.2	287.0 ± 5.2	389.6 ± 5.6	451.4 ± 5.0	499.7 ± 4.7	525.2 ± 7.7	556.6	580
Mean annual growth (mm)					152.9 ± 4.2	134.1 ± 4.6	102.6 ± 5.5	57.0 ± 4.2	43.0 ± 4.7	20.4 ± 1.8	21.1	23.4

$P < 0.0001$). A von Bertalanffy growth curve with the parameters $L_\infty = 479.5 \pm 8.7$, $k = 0.486 \pm 0.027$ and $t_0 = 0.560 \pm 0.040$ describes growth for male spotted sucker, and a curve with parameters of $L_\infty = 481.7 \pm 6.1$, $k = 0.341 \pm 0.017$, and $t_0 = 0.352 \pm 0.063$ fit growth for females (Fig. 2).

Over 77% of captured notchlip redhorse were between the ages of five and seven; however, fish ranged from 3 to 10 years of age (Table 4). No difference in growth rate between the sexes ($F = 3.59$, d.f. = 1, 545 and $P = 0.06$) was detected. Therefore, von Bertalanffy growth parameters of $L_\infty = 464.6 \pm 4.1$, $k = 0.571 \pm 0.018$ and $t_0 = 0.562 \pm 0.021$ were estimated for the combined growth curve (Fig. 2). Back calculated total lengths show growth in notchlip redhorses slows after fish reach approximately 361.4 ± 3.3 mm TL at age three.

Robust redhorse ranged in age from 3 to 13, but the majority of individuals captured in the spawning aggregations (approximately 65%) were between the ages of six and 10(Tables 5 and 6). Males and females differed in their growth rates ($F = 19.21$, d.f. = 1, 1234 and $P < 0.0001$). A von Bertalanffy growth curve with parameters of $L_\infty = 626.6 \pm 2.2$, $k = 0.4647 \pm 0.006$ and $t_0 = 0.5857 \pm 0.012$ was fitted for males, while a curve with the parameters of $L_\infty = 662.4 \pm 3.5$, $k = 0.4043 \pm 0.009$ and $t_0 = 0.5357 \pm 0.023$ was used to described growth for females (Fig. 2). Back calculated length at age indicates that young robust redhorse grow rapidly, reaching almost 460 mm TL by age three, but growth slowed to approximately 20–30 mm·year^{-1} after age five (Tables 6 and 7).

Discussion

There are numerous factors that may allow ecologically similar species coexist. Differences in life history strategies can allow species to avoid competition for the same resources by diversifying how those resources are used (Winemiller & Rose 1992; Basset 1995, 1997). Savannah River catostomids do not seem to show a large amount of divergence in their trophic specialisations and as such may rely on other specialisations, such as differences in life history strategies, to coexist. An examination of the size and age structure of populations and the growth patterns of individuals within those populations can provide insight into these differences (Table 7). In the Savannah River, robust redhorse seems to have adopted a strategy entailing relatively late maturity, long life and a large body size presumably with high fecundity. Northern hogsucker would then seem to have adopted a strategy at the other extreme consisting of early maturity short lifespan, and small body size. The other two species appear to fall between these two extremes. However, additional data on fecundity and investment per individual progeny (Winemiller & Rose 1992) would be required to determine if these initial conclusions are valid.

The catostomid species collected from main channel gravel bars in the Savannah River possessed relatively discrete size distributions. Body size is an important consideration in the coexistence of species within a guild (Huxley 1942; Hutchinson & MacArthur 1959; Basset 1995, 1997). Differences in body size among otherwise ecologically similar species enables the species to partition resources because of the way they forage and use their environment, i.e. smaller species tend to have small home ranges that are move intensively used and vice versa for larger species (Basset 1995, 1997). Grabowski & Isely (2006) found that robust redhorse in the Savannah River restrict their daily movements over approximately 1.0 rkm. However, data on the movement and habitat use patterns of the other species in this assemblage are not currently available. Interspecific differences in body

Table 4. Mean (±SE) back-calculated total length (TL) at each annulus of notchlip redhorse from the Savannah River, South Carolina–Georgia.

			TL (mm) at capture		Back calculated TL (mm) at age									
Age group	Year class	*N*	Mean	Range	1	2	3	4	5	6	7	8	9	10
0	–	0												
I	–	0												
II	–	0												
III	2001, 2002	4	375.0 ± 17.7	338–421	135.3 ± 8.9	278.8 ± 21. 3	375.0 ± 17.6							
IV	2000, 2001	31	416.7 ± 2.5	388–438	137.0 ± 3.3	298.2 ± 5.2	386.1 ± 4.3	416.7 ± 2.5						
V	1999, 2000	25	435.2 ± 3.2	408–468	124.4 ± 4.3	266.5 ± 5. 3	359.5 ± 5.8	406.1 ± 4. 8	435.2 ± 3.2					
VI	1998	24	442.7 ± 3.4	410–474	124.2 ± 4.0	253.5 ± 6.0	344.5 ± 6.4	392.7 ± 5.5	422.2 ± 4.3	442.7 ± 3. 4				
VII	1997	12	448.2 ± 4.2	426–473	116.6 ± 3.7	252.9 ± 7.7	339.7 ± 9.8	382.9 ± 8.7	413.5 ± 6.4	432.9 ± 5.2	448.2 ± 4.2			
VIII	1996	6	468.2 ± 6.6	433–473	120.6 ± 10.3	245.1 ± 11. 5	341.4 ± 5.1	388.3 ± 1.9	417.6 ± 3.5	438.8 ± 4.3	455.1 ± 6.0	468.2 ± 6.6		
IX	–	0	–		–	–	–	–	–	–	–	–	–	–
X	1994	1	539		138.8	317.5	373.9	420.5	449.6	474.9	492.4	511.8	525.4	539
Mean TL (mm) at age					127.6 ± 2.0	271.1 ± 3.4	361.4 ± 3.3	402.4 ± 2. 5	425.5 ± 2.5	440.2 ± 2.6	440.7 ± 3.9	511.8	525.4	539
Mean annual growth (mm)					127.6 ± 2.0	138.0 ± 4.0	85.9 ± 2.3	39.2 ± 1.8	26.4 ± 1.5	18.8 ± 1.2	15.7 ± 1.1	19.4	13.6	13.6

Table 5. Mean (±SE) back-calculated total length (TL) at each annulus of male robust redhorse from the Savannah River, South Carolina–Georgia.

			TL (mm) at capture		Back calculated TL (mm) at age											
Age group	Year class	*N*	Mean	Range	1	2	3	4	5	6	7	8	9	10	11	12
0	–	–	–	–												
I		–	–	–												
II		–	–	–												
III	1999	2	455.0 ± 5.0	450–460	107.2 ± 7.5	316.7 ± 22.7	455.0 ± 5.0									
IV	2000, 2001	2	497.0 ± 9.0	488–506	106.0 ± 1.4	322.2 ± 10.0	458.3 ± 9.0	497.0 ± 9.0								
V	1997, 1999, 2000	13	532.4 ± 2.2	522–546	113.0 ± 3.8	324.9 ± 7.5	452.4 ± 4.8	505.8 ± 2.0	532.4 ± 2.2							
VI	1996, 1998, 1999	16	564.7 ± 2.8	550–590	112.3 ± 4.4	287.5 ± 9.6	437.4 ± 7.3	506.6 ± 4.2	542.2 ± 3.5	564.7 ± 2.8						
VII	1995, 1997, 1998	28	590.2 ± 2.6	572–640	106.8 ± 1.8	283.1 ± 6.5	434.4 ± 4.6	496.7 ± 3.6	540.3 ± 2.8	569.0 ± 2.6	590.2 ± 2.6					
VIII	1994, 1996, 1997	22	613.7 ± 3.0	592–636	120.0 ± 4.8	306.5 ± 7.4	447.9 ± 6.0	509.8 ± 4.6	545.9 ± 3.5	573.2 ± 3.0	594.7 ± 3.0	613.7 ± 3.0				
IX	1995, 1996	15	626.8 ± 3.8	602–656	107.5 ± 1.7	290.1 ± 7.9	434.2 ± 6.2	502.7 ± 5. 9	537.8 ± 5.8	566.6 ± 5. 5	591.2 ± 4.7	609.3 ± 4.2	626.8 ± 3.8			
X	1992, 1994, 1995	15	640.5 ± 4.7	612–665	102.9 ± 2.3	284.4 ± 6.5	429.8 ± 6.0	497.6 ± 6.0	533.6 ± 6.2	561.7 ± 5. 8	585.6 ± 5.6	606.0 ± 5.2	624.5 ± 4.9	640.5 ± 4.7		
XI	1993, 1994	6	647.8 ± 9.1	630–692	106.7 ± 2.6	285.4 ± 7.0	419.7 ± 4.1	486.8 ± 9.3	529.0 ± 14.0	558.1 ± 13.2	580.1 ± 12.2	601.7 ± 11.5	618.4 ± 9.9	633.5 ± 8.8	647.8 ± 9.1	
XII	1993	1	652	–	111.9	239.0	387.8	443.0	503.2	540.0	563.4	581.8	600.2	620.2	635.3	652
Mean TL (mm) at age					110.3 ± 1.3	294.5 ± 3.1	435.9 ± 2.4	501.4 ± 1.7	538.6 ± 1.7	566.9 ± 1.8	589.5 ± 1.8	609.3 ± 2.4	623.5 ± 3.1	637.7 ± 4.0	646.0 ± 7.9	652
Mean annual growth (mm)					110.3 ± 1.3	167.1 ± 5.1	129.0 ± 4.1	59.5 ± 2.1	33.4 ± 1.2	25.2 ± 0.8	20.3 ± 0.8	18.0 ± 0.8	16.2 ± 1.1	14.4 ± 1.2	14.4 ± 1.2	16.7

Table 6. Mean (±SE) back-calculated total length (TL) at each annulus of female robust redhorse from the Savannah River, South Carolina–Georgia.

			TL (mm) at capture		Back calculated TL (mm) at age												
Age group	Year class	*N*	Mean	Range	1	2	3	4	5	6	7	8	9	10	11	12	13
0	–	–	–	–													
I	–	–	–	–													
II	–	–	–	–													
III	–	–	–	–													
IV	–	–	–	–													
V	–	–	–	–													
VI	1996, 1998, 1999	3	562.1 ± 12.3	538–578	110.0 ± 11.8	267.5 ± 18.4	443.4 ± 31.7	512.9 ± 26.1	546.1 ± 18.7	562.1 ± 12.3							
VII	1995, 1997	3	580.3 ± 5.6	550–586	123.3 ± 13.9	295.6 ± 14.1	436.6 ± 16.3	497.4 ± 13.0	531.1 ± 11.6	558.7 ± 7.1	580.3 ± 5.6						
VIII	1996	1	650	–	126.6	319.8	450.7	519.4	560.2	605.3	635.3	650.0					
IX	1995, 1996	7	645.5 ± 6.3	623–678	114.6 ± 5.2	297.4 ± 9.5	429.8 ± 7.1	496.1 ± 8.2	544.3 ± 7.0	580.8 ± 6.4	609.6 ± 6.5	628.3 ± 6.3	645.5 ± 6.3				
X	1992, 1994, 1995	9	651.4 ± 8.2	621–680	110.1 ± 3.6	293.0 ± 11.6	435.9 ± 13.4	501.6 ± 12.6	548.1 ± 13.6	576.7 ± 12.3	600.3 ± 10.9	619.2 ± 9.5	636.9 ± 9.0	651.4 ± 8.2			
XI	1991, 1993, 1994	7	668.9 ± 7.2	641–690	109.2 ± 5.4	293.0 ± 16.0	441.7 ± 14.3	510.6 ± 13.1	553.9 ± 11.5	587.1 ± 10.9	611.1 ± 10.2	628.8 ± 8.2	645.5 ± 7.4	659.2 ± 6.9	668.9 ± 7.2		
XII	1992, 1993	3	685.3 ± 13.9	662–710	98.1 ± 1.9	281.6 ± 23.7	424.9 ± 14.6	504.9 ± 10.6	552.1 ± 9.2	576.9 ± 8.0	599.8 ± 6.6	618.4 ± 6.7	635.8 ± 7.1	654.6 ± 8.8	670.4 ± 8.4	685.3 ± 13.9	
XIII	1991	1	701	–	103.4	264.8	415.2	484.8	543.5	574.7	605.9	629.7	646.2	668.3	682.9	692.1	701.3
Mean TL (mm) at age					111.2 ± 2.4	290.8 ± 5.6	435.4 ± 5.5	503.3 ± 5.1	547.4 ± 4.8	577.6 ± 4.5	605.0 ± 4.5	625.3 ± 4.1	641.6 ± 3.9	655.5 ± 4.5	670.6 ± 5.0	687.0 ± 10.0	701.3
Mean annual growth (mm)					111.2 ± 2.4	179.6 ± 5.3	144.6 ± 4.6	67.7 ± 2.2	44.2 ± 2.0	30.2 ± 1.6	24.9 ± 1.0	18.5 ± 1.0	17.2 ± 1.3	15.2 ± 1.3	11.9 ± 1.0	13.5 ± 4.8	9.2

Table 7. Maximum observed age and length, age and length at maturity, Von Bertanlanffy growth curve parameters, instantaneous (*Z*) and annual (*A*) mortality rate estimates, and time and temperature of observed spawning activity of four catostomid species in the Savannah River, Georgia–South Carolina. All parameter estimates are reported ±SE.

					Von Bertanlanffy growth curve parameters			Mortality rate estimates		Spawning period†	
Species	Maximum observed age	Maximum observed length (mm TL)	Age at maturity	Length at maturity (mm TL)	L_∞	*k*	t_0	Z	*A*	Time	Temperature (°C)
Northern hogsucker	5	274	3	>190	329.7 ± 25.3	0.332 ± 0.049	0.373 ± 0.063	0.733 ± 0.377	0.520	14 March–1 June‡	12.7–23.3‡
Spotted sucker (female)	8	580	3–5	>366	481.7 ± 6.1	0.341 ± 0.017	0.352 ± 0.063	0.852 ± 0.146	0.573	13–25 April	14.4–19.7
Spotted sucker (male)	6	529	2–4	>380	479.5 ± 8.7	0.486 ± 0.027	0.560 ± 0.040	0.852 ± 0.146	0.573	13–25 April	14.4–19.7
Notchlip redhorse	10	539	3–4	>341	464.6 ± 4.1	0.571 ± 0.018	0.562 ± 0.021	0.624 ± 0.1 50	0.464	2 April–9 May	12.7–19.7
Robust redhorse (female)	13	701	6–7	>562	662.4 ± 3.5	0.404 ± 0.009	0.536 ± 0.023	0.508 ± 0.126	0.398	2 May–18 May	17.6–21.8
Robust redhorse (male)	12	652	3–4	>387	626.6 ± 2.2	0.465 ± 0.006	0.586 ± 0.012	0.508 ± 0.126	0.398	2 May–18 May	17.6–21.8

†From Grabowski and Isely (2007).
‡Indicates time and temperature northern hogsucker were present on gravel bars. Spawning was not observed in this species.
TL, total length.

size also may play a role in the observed spatial and temporal partitioning of the limited spawning habitat available to catostomids in the Savannah River. Spotted sucker, notchlip redhorse and robust redhorse each exhibited preferences for current velocities, water depth and mean substrate particle size that were discrete from one another (Grabowski & Isely 2007a). For example, robust redhorse, the largest species of the assemblage, preferred areas with the largest substrate particle sizes and highest flow on the available spawning habitat. It was also the last species of the assemblage to spawn. Additional research is needed to determine what significance, if any, body size has on the coexistence of catostomids in the Savannah River and in other river systems.

The high mortality rate consistently observed across the four species Savannah River catostomids was surprising given the distinct differences in body size and growth rates exhibited among the species. We would have expected northern hogsucker to exhibit the highest mortality rate and robust redhorse to exhibit the lowest with the remaining species exhibiting moderate annual and instantaneous mortality. There are many possible reasons for the levels of mortality in Savannah River catostomids. The Savannah River is a system heavily impacted by urbanisation and other changes of land use patterns within its watershed (Marcy et al. 2005), cold water hypolimnetic discharge (Paller & Saul 1996), disruptions to the natural flow regime (Grabowski and Isely, 2007b), and exotic species introductions (Marcy et al. 2005). However, most of these impacts would tend to disproportionally affect younger age classes and would not be evident in a short-term study focusing on older, sexually mature individuals. The reason for the high mortality rate across species is likely because of bias in both field collections and scale microstructure analysis. Sampled spotted sucker, notchlip redhorse and robust redhorse were mostly sexually mature individuals that were often observed spawning prior to sampling. Therefore, the smaller, immature size classes of these species were not represented in our samples. This combined with a likely underestimation of the age of older individuals (Beamish 1973; Beamish & McFarlane 1983; Scoppettone 1988; Sylvester & Berry 2006) may have contributed to the high mortality rates derived from catch curve data and the lack of differentiation in mortality rates among species.

Savannah River northern hogsucker appears to fall into the category of short-lived, fast-growing species. Previous age and growth studies of northern hogsucker have focused on northern populations (Raney & Lachner 1946a; Carlander 1969). Although our data generally agree with published reports for size at early ages, northern hogsucker in the Savannah River appear to grow considerably slower than conspecifics in New York, Oklahoma and Virginia. Published reports also indicate that males grow faster through age four, and that females grow faster thereafter (Raney & Lachner 1946a; Carlander 1969). We did not observe differences in growth between the sexes. However, our ability to detect such a difference, if present, was limited by age composition and sample size. Northern hogsuckers are generally associated with smaller creeks and rivers (Etnier & Starnes 1993; Jenkins & Burkhead 1993; Marcy et al. 2005). Therefore, it is possible that individuals within populations confined to the main channel of a large river such as the Savannah do not grow as fast. The modified temperature regime of the Savannah River because of hypolimnetic discharge (Paller & Saul 1996) may contribute to the low growth rates observed in this study. It also is possibility that larger individuals do not occupy the gravel bar habitats sampled in our study. A more thorough study comparing growth across different habitats regionally or within the Savannah River basin may be warranted for this species.

Like northern hogsucker, spotted sucker appears to be a short-lived, fast-growing species. Growth rates in the Savannah River are consistent with those reported for populations in Oklahoma and Minnesota (Carlander 1969; Pflieger 1975). These previous studies did not note a difference in growth rate between the sexes, as found in this study. Both sexes appeared to grow at similar rates through their first 3 years of life, after which females tended to grow faster. The initiation of sex-specific growth corresponds to the attainment of sexual maturity at age three reported for this species by Pflieger (1975).

Notchlip redhorse in the Savannah River seem to employ a life history strategy featuring an intermediate lifespan and growth rate. We did not observe any differences in size at age between males and females. We were unable to locate any previous studies of the growth of this species for comparison. However, our results agree with growth rates reported for silver redhorse *M. anisurum*, the presumed sister species of notchlip redhorse (Jenkins 1970; Jenkins & Burkhead 1993), in Alabama (Hackney et al. 1971), Iowa (Meyer 1962), and Missouri (Carlander 1969). Both species also reach a maximum age of 10 years. Notchlip redhorse in the Savannah River appear to reach sexual maturity at a younger age (age: 3–4) than that reported for silver redhorse (age: 5–6: Hackney et al. 1971).

Robust redhorse is the largest catostomid species in south-eastern Atlantic Slope drainages (Marcy et al. 2005) and as such, we hypothesised it has employed a life history strategy involving slow growth and long life spans. The results of this study would seem to suggest that robust redhorse do not exhibit a life history pattern dramatically different from notchlip redhorse in the Savannah River. However, the underestimation of age from catostomid scales has been well documented (Beamish 1973; Beamish & McFarlane 1983; Scoppettone 1988; Sylvester & Berry 2006). Presumably, many of the robust redhorse in our sample were older than we report. Maximum ages, growth rates and mortality rates should be interpreted as conservative estimates. Our study demonstrates that robust redhorse reach a maximum age of at least 13 years, and have the potential to be much older. Robust redhorse have been estimated to be as old as 27 based upon analysis of annuli present on opercles (R. E. Jenkins, personal communication).

Early rapid growth of robust redhorse suggests this species may delay sexual maturation to more quickly attain large sizes. This strategy is thought to be employed by sturgeons and other large, long-lived fishes (Winemiller & Rose 1992). Robust redhorse tend to be smaller than spotted sucker or notchlip redhorse at the end of their first year of growth, but surpass both species by the end of the second year. We speculate the accelerated growth in the second year may correspond to the development of the crushing, molariform pharyngeal teeth characteristic of this species (Marcy et al. 2005). The development of these specialised structures allows robust redhorse to exploit hard-shelled invertebrate prey species inaccessible to the other catostomids (Marcy et al. 2005). Additional information on the developmental sequence and juvenile ecology of this species is necessary to test this hypothesis. While there are no comparable studies on the growth of robust redhorse in the literature, our results indicate robust redhorse grow considerably faster than river redhorse *Moxostoma carinatum* (Cope), another large-bodied molariform redhorse, in Oklahoma and Missouri (Carlander 1969).

The range of life history strategies employed by Savannah River catostomids represents the range of life history strategies in the family as a whole (Beamish 1973; Cooke et al. 2005). Although catostomids are common fishes that occur in freshwater habitats throughout North America, relatively little has been published regarding basic life history parameters related to age, growth and mortality (Cooke et al. 2005) or how these parameters may vary in response to location or assemblage structure. Filling this knowledge void has become critical to conservation efforts, as an increasing number of catostomid species are considered vulnerable, threatened or endangered (Cooke et al. 2005) and new species within the family are discovered or recognised (Nelson et al. 2004).

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