

## Articles

# Age, Growth, and Reproductive Biology of Three Catostomids From the Apalachicola River, Florida

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## Abstract

Riverine catostomids can show a wide range of interspecific variation in life-history characteristics. Understanding these differences is an important consideration in evaluating the sensitivity of these fishes to disturbance and in formulating effective conservation strategies, particularly when dealing with an assemblage consisting of multiple species within a watershed. We collected Apalachicola redhorse *Moxostoma* n. sp. cf. *poecilurum* ( $n = 125$ ), spotted sucker *Minytrema melanops* ( $n = 94$ ), and quillback *Carpoides cyprinus* ( $n = 94$ ) to determine age, growth, and reproductive biology of spawning catostomids in the Apalachicola River, Florida, during 2007. Quillback was the smallest in total length at age; longest-lived; most fecund; and produced the smallest eggs. Apalachicola redhorse was the largest in body size; had an intermediate life span; and produced the fewest yet largest eggs. Spotted sucker was more similar to Apalachicola redhorse in most characteristics. Growth during ages 1–3 in all three species seemed to be negatively related to the proportion of observations of extreme flow, both high ( $Q_{90}$ ) and low ( $Q_{10}$ ), per year and a positive response in growth rate to high flows ( $>Q_{75}$  but  $< Q_{90}$ ). However, Apalachicola redhorse and spotted sucker growth was more sensitive to flow conditions than that of quillback. Our results suggest the life histories and ecological response of Apalachicola River catostomids to flow regulation are important components for developing strategies that incorporate the needs of these fishery resources into an ecosystem-based management approach.

Keywords: egg composition; environmental flows; life-history strategy; reproductive ecology; riverine fish conservation

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## Introduction

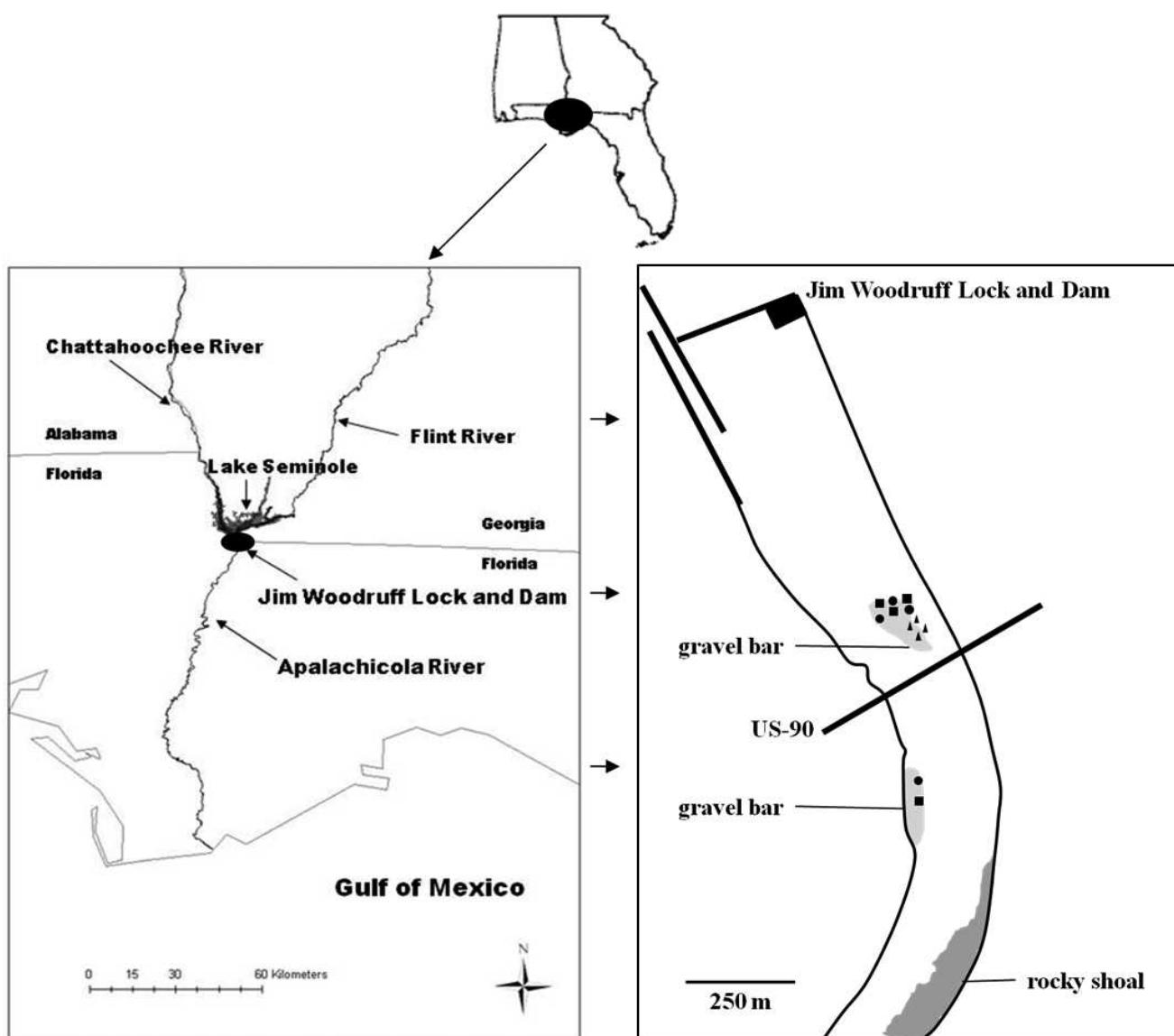
Human-induced variability of flow regimes has been implicated as a major factor in the decline of freshwater fish populations in North America (Warren et al. 1997, 2000; Cooke et al. 2005). Diel fluctuations, drastic reductions of flow over a short period of time, or other alterations to the natural flow regime may alter habitat suitability and availability; negatively affect reproductive success; and influence growth, survival, and recruitment of early life-history stages (Poff et al. 1997; Grabowski and Isely 2007; Peterson and Jennings 2007). However, there is often a wide range of sensitivity to disturbance and habitat degradation among species within an assemblage, even among relatively closely related species (Sparks 1995; Magalhaes et al. 2003; Zeug and Winemiller 2008). The life-history strategies of riverine fishes likely play an important role in determining this sensitivity. For example, in regulated rivers where prolonged, low-flow conditions are common, the populations of many short-lived species may become depleted, while little effect is observed on the populations of longer lived fishes (Mueller and Wydoski 2004; Bonvechio and Allen 2005; Sammons and Maceina 2009). The early life-history stages of both groups may experience high mortality, but the population structure of longer lived species may be more stable in response to repeated weak or missing year classes (Peterson and Jennings 2007). However, species-specific life-history traits, such as migratory behavior, reproductive strategy, or age-specific habitat requirements, and intraspecific variation among conspecifics that inhabit different river basins render it difficult to make generalizations such as this. The interaction of life-history characteristics with environmental factors on population-level processes is not well-understood for most members of riverine fish assemblages, which makes it difficult to predict how these species might respond to disturbance or degradation. This is likely due in large part to the fact that the basic biology of the majority of species comprising a given assemblage is poorly known.

Catostomids are a diverse family of primarily North American fishes that often dominate riverine fish assemblages in terms of number of species (Mettee et al. 1996; Marcy et al. 2005; Quist et al. 2005) and biomass (Jenkins and Burkhead 1994; Richardson et al. 2000). Many catostomid species, particularly those endemic to a single river basin, are believed to have suffered significant population declines over the past 100–200 y (Gilbert 1992; Mettee et al. 1996; Thieme et al. 2001; Cooke et al. 2005; Henne et al. 2007), primarily due to a combination of altered hydrological regimes, habitat fragmentation, past exploitation patterns, and changing land-use practices within watersheds (Cooke et al. 2005). Despite the ecological importance and decline of catostomids in North American freshwater systems, the group has been virtually ignored by fishery scientists, which has resulted in an inadequate information base that has hampered conservation efforts (Cooke et al. 2005). This lack of data has also led to the perception that catostomid species inhabiting a river system are

similar in their behavior, ecology, and life-history strategies, when in fact dramatic differences often exist (Cooke et al. 2005; Grabowski and Isely 2007; Grabowski et al. 2008) with the potential for different responses to both disturbance and conservation efforts. This perception of similarity among species has proven problematic in the southeastern United States, where there is a high diversity of catostomids, not only at the regional or watershed scale (Jenkins and Burkhead 1994; Mettee et al. 1996; Marcy et al. 2005), but also at more localized scales within a river system (Grabowski and Isely 2007). For example, both Mettee et al. (1996) and Boschung and Mayden (2004) documented 23 catostomid species in Alabama. Of these, 15 species inhabit the river basins of the northern Gulf of Mexico from the Mississippi River to Florida panhandle river basins (Mettee et al. 1996; H. L. Bart, Jr, Tulane University Museum of Natural History, personal communication). Among these species are many that are endemic or at the southernmost limit of their ranges; yet, very little is known about the basic biology and life-history characteristics of these species. Given the increased demand on water resources due to unprecedented growth and urban development in the northern Gulf coastal region (Gibson et al. 2005), acquiring detailed geographic range, habitat requirements, and life-history information is essential in the development of management strategies to ensure long-term viability of catostomid assemblages in north Gulf Coast drainages, such as the Apalachicola River, Florida.

In the Apalachicola River drainage, the catostomid assemblage contains at least two to four endemic species and several species at the limit of their geographic distributions (Mettee et al. 1996; Peterson et al. 2000; H. L. Bart, Jr, personal communication). For example, chubsuckers *Erimyzon* spp., spotted sucker *Myomyrus melanops*, quillback *Carpioles cyprinus*, and highfin carpsucker *Carpioles velifer* are distributed throughout eastern North America, generally within and east of the Great Lakes and Mississippi River basin (Lee et al. 1980; Marcy et al. 2005), but these species are at the southeastern limits of their distribution in the Apalachicola River (Boschung and Mayden 2004; Young et al. 2010). The populations of the two *Carpioles* species, along with those in adjacent coastal rivers, may constitute separate species that are distinct from populations in the Mississippi River and Great Lakes drainages (Mettee et al. 1996; H. L. Bart, Jr, personal communication). Apalachicola redhorse *Moxostoma* n. sp. cf. *poecilurum* is an undescribed species endemic to the Apalachicola River drainage (Gilbert 1992; Mettee et al. 1996; R. E. Jenkins, Roanoke College, personal communication). Only a few general reports of habitat, distribution, and life history are available for the Apalachicola redhorse, and limited data are available for catostomids generally in northern Gulf Coast drainages, such as the Apalachicola River. Therefore, our objectives were to characterize the age, growth, and reproductive biology of the catostomid species found below Jim Woodruff Lock and Dam (JWLD) in the Apalachicola River and to evaluate the effects of flow variability on the growth of these species using back-calculated lengths at age.





**Figure 1.** Location of study site within the southeastern United States and within the Apalachicola River Basin. Study reach below Jim Woodruff Lock and Dam shown to scale with approximate capture locations for catostomids indicated by species. Solid circles denote Apalachicola redhorse *Moxostoma n. sp. cf. poecilurum* capture sites. Solid squares denote spotted sucker *Minytrema melanops* capture sites. Solid triangles denote quillback *Carpioles cyprinus* capture sites.

## Methods

### Study area

The Apalachicola River has the highest discharge among Florida rivers, and the basin is home to the one of the most diverse fish faunas east of the Mississippi River, with  $\geq 99$  freshwater fish species, including 8 endemic species (Neely et al. 2007). The system drains a 50,500-km<sup>2</sup> area in Alabama, Florida, and Georgia. It is highly impacted by anthropogenic activities, including six lock-and-dam facilities for navigation, flood control, and hydro-electric production (Gibson et al. 2005). The river originates at the confluence of the Flint and Chattahoochee rivers approximately 3.0 km upstream of JWLD and flows without obstruction below the dam for 171 km to Apalachicola Bay, an inlet of the Gulf of

Mexico. Jim Woodruff Lock and Dam is a run-of-the-river lock and dam located in the central panhandle of Northwest Florida near the Georgia border (Figure 1). Our research focused on an approximately 1.5-km reach immediately downstream of JWLD that included the tailrace of the dam, two large gravel bars, and a rocky shoal marking the downstream edge of the reach (Figure 1).

### Data collection

We captured catostomids within the 1.5-km reach immediately below JWLD during February–April 2007, using boat electro-fishing. Captured catostomids were measured (mm total length [TL]) and weighed (g). We determined sex based upon gamete expression and presence of nuptial tubercles for Apalachicola redhorse

and spotted suckers, and only upon gamete expression for quillback because both sexes exhibit fine tuberculation. We removed a minimum of three scales from above the lateral line to determine age. In addition, we sacrificed a representative subsample of each species to collect ovaries and otoliths (Apalachicola redhorse: 12 females, 11 males, 1 juvenile; spotted sucker: 18 females, 25 males, 2 juveniles; quillback: 18 females, 4 males). The decision to sacrifice a limited number of individuals was based on the lack of information regarding population sizes of these species, especially Apalachicola redhorse. In addition, we photographed representative specimens to confirm species identification, and we preserved several individuals for curation (4 Apalachicola redhorse, 3 quillback). These voucher specimens were deposited at the North Carolina Museum of Natural Sciences in Raleigh, North Carolina under the catalog numbers NCSM 45829 (Apalachicola redhorse) and NCSM 45842 (quillback).

We pressed scales into acetate using the standard methods described by Devries and Frie (1996). These acetate impressions were magnified using a digital microfiche reader and saved as digital images, which were then used to determine age and to back-calculate TL at age (mm) for each scale annuli using ImageJ 1.44 (Abramoff et al. 2004). We sectioned sagittal otoliths along the sagittal plane at a width of 0.5 mm. Otolith sections were polished to improve visual quality, and then examined using a microscope equipped with a digital camera (Nikon Corporation, Melville, NY). Annuli were identified as the distal edge of the transition from opaque to translucent zones. All data used in length-at-age and growth analyses were acquired from scales due to the limited number of fish sacrificed. We used otoliths to validate accuracy and bias of ages from scales and to analyze relationships between maternal age and fecundity, egg size, and percent lipid content of eggs. Aging structures were examined by two independent readers, and discrepancies were resolved by a third reader.

We acquired flow data from the U.S. Geological Survey streamflow-gaging station 0235800 located near the US-90 crossing in Chattahoochee, Florida (Figure 1). Discharge data collected at 15-min intervals during 1992–2005, a period that encompasses ages 1–3 of the catostomids assessed in this study, were downloaded from the online Instantaneous Data Archive (available at <http://ida.water.usgs.gov>). We determined streamflow quantiles from the flow data for the entire 13-y period; we defined high flows as being between 682 m<sup>3</sup>/s (Q<sub>25</sub>) and 1,158 m<sup>3</sup>/s (Q<sub>10</sub>), low flows as being between 280 m<sup>3</sup>/s (Q<sub>75</sub>) and 190 m<sup>3</sup>/s (Q<sub>90</sub>), normal flows as being between Q<sub>25</sub> and Q<sub>75</sub>, and extreme flows those that exceeded Q<sub>10</sub> or dropped below Q<sub>90</sub>. The proportion of observations that fell into each of these categories was determined for each year and used in further analysis (Tables S1–S2, *Supplemental Material*).

We estimated instantaneous mortality rate ( $Z$ ) for each species from the slope of the descending leg of a catch curve and converted it to annual mortality ( $A$ ) as described by Ricker (1975).

We removed whole ovaries by dissection and then weighed them. A subsample of 100 eggs per individual was weighed to determine average egg weight. Fecundity was then calculated by dividing total ovary weight (g) by average egg weight (g). Females with partially spawned ovaries were not included in fecundity estimates, but were used for comparison of average egg weight between species. We compared egg size of individuals and mean egg size of each species using the values of total mass (g) per 100 eggs.

We determined lipid content of the eggs using the gravimetric method (Folch et al. 1957). Briefly, a portion of each ovary (wet weight = 24.5 ± 4.0 g; mean ± SD) was freeze-dried and pulverized with mortar and pestle. The lipids were extracted from dried egg samples (dry weight = 10.0 ± 1.7 g; mean ± SD) using ~5.0 mL of a 2:1 chloroform:methanol solution. The lipid-solvent solution was separated from the egg sample using filter paper and the remaining egg mass dried. We calculated lipid weight by subtracting post-lipid-extraction dry weight from pre-extraction dry weight, and we then calculated percent lipid content by dividing lipid weight by pre-extraction dry weight. We used percent lipid content as the standardized variable in comparison of egg lipid content between species.

## Data analyses

We estimated length at age from scales by using back calculation. We measured scale radius and radius to each growth increment in a straight line at a 45° angle from the focus. Back-calculated length at previous age was determined and corrected using the Fraser–Lee method (Fraser 1916; Lee 1920). This has been suggested for catostomid studies due to delayed squamation (Meyer 1962; Hackney et al. 1971; Hogue and Buchanan 1977; White 1977; Fuiman 1979; Fuiman and Witman 1979; Kay et al. 1994). We developed a von Bertalanffy growth curve (von Bertalanffy 1938) from the back-calculated length-at-age data for each species, and for females and males within species. Growth rates were constructed by fitting calculated lengths to the von Bertalanffy growth model:

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

where  $L_t$  is the TL at time  $t$ ;  $L_{\infty}$  is the maximum theoretical total attainable length;  $k$  is the growth coefficient; and  $t_0$  is the time when length would be zero (von Bertalanffy 1938). We used analysis of covariance (ANCOVA) to assess differences in growth between males and females within species. Back-calculated lengths, growth curves, and sex-based differences in growth were calculated following methods detailed by Isely and Grabowski (2007). We used the residuals from the von Bertalanffy growth curves to assess the effects of flow on growth using a repeated-measures ANCOVA, with species and flow variables as fixed effects and individuals as a subject effect. Residuals were used because they provide an indication of whether an individual reached a larger or smaller size at age than what was predicted by the von Bertalanffy growth model for that particular species.



**Table 1.** Mean ( $\pm$  SD) total length (TL) and weights (W) of male and female Apalachicola redhorse *Moxostoma* n. sp. cf. *poeциlurum*, spotted sucker *Minytrema melanops*, and quillback *Carpoides cyprinus* captured from the Apalachicola River, Florida, during February–April 2007. Parameter estimates ( $\pm$  SE) for the von Bertalanffy growth function are presented for males and females of each species.

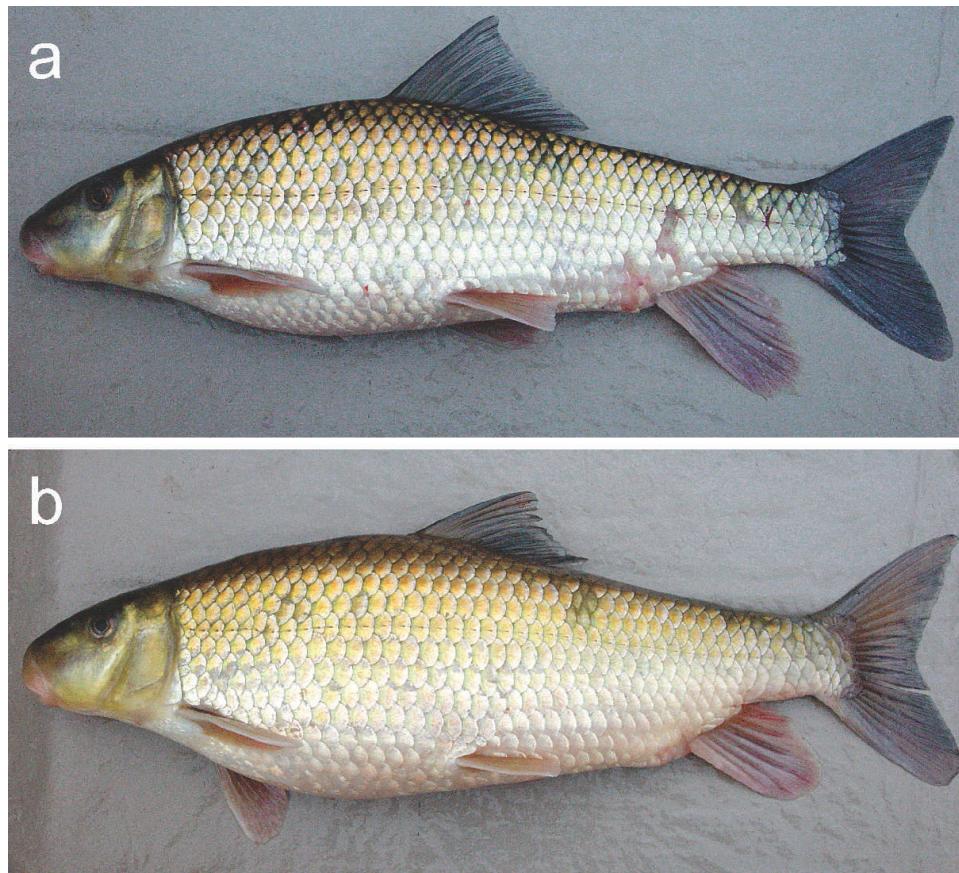
Species	Sex	n	Mean TL (mm)	Mean W (g)	Von Bertalanffy parameter estimates		
					$L_\infty$	k	$t_0$
Apalachicola redhorse	male	103	437 $\pm$ 33	1,430 $\pm$ 408	478.4 $\pm$ 8.1	0.39 $\pm$ 0.02	0.19 $\pm$ 0.05
	female	22	457 $\pm$ 33	1,540 $\pm$ 316	478.9 $\pm$ 14.6	0.49 $\pm$ 0.05	0.27 $\pm$ 0.09
Quillback	male	44	401 $\pm$ 38	1,003 $\pm$ 300	415.3 $\pm$ 8.2	0.40 $\pm$ 0.03	-0.09 $\pm$ 0.11
	female	50	425 $\pm$ 41	1,245 $\pm$ 337	433.2 $\pm$ 5.6	0.40 $\pm$ 0.02	-0.08 $\pm$ 0.08
Spotted sucker	male	68	422 $\pm$ 23	958 $\pm$ 161	445.3 $\pm$ 9.7	0.44 $\pm$ 0.03	0.16 $\pm$ 0.07
	female	26	446 $\pm$ 49	1,058 $\pm$ 336	545.8 $\pm$ 26.0	0.27 $\pm$ 0.03	0.02 $\pm$ 0.12

We used chi-square to test for differences in age-class frequency between species. Number of individuals per age-class was enumerated by species, and then divided by sample size per species to calculate percentage of sample at each age-class. The percentage was used to derive a standardized count of each age-class per 100 individuals for statistical analysis. We used analysis of variance to test the null hypothesis that the three species were similar in their fecundity, egg size, and percent lipid composition. We used Pearson's correlation to evaluate any relationships between maternal age, length, weight, or condition with fecundity, egg size, or percent lipid

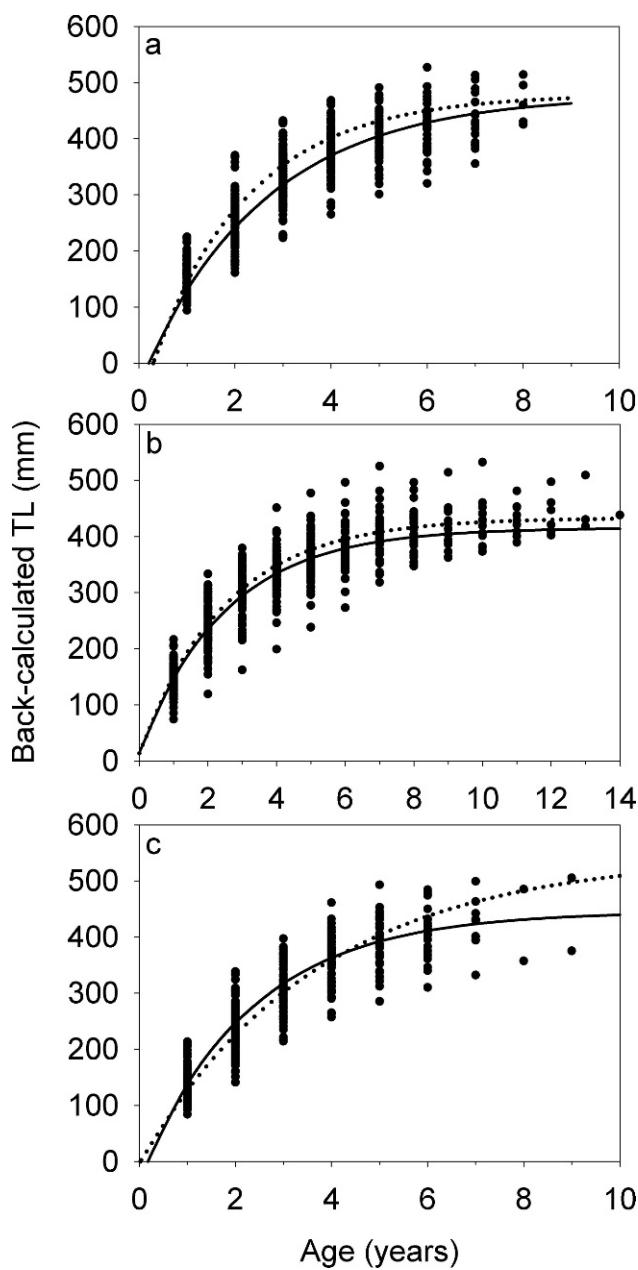
composition. We used SAS 9.0 (SAS Institute, Inc., Cary, NC) to perform all statistical analyses, with a significance level of  $\alpha = 0.05$  for all comparisons.

## Results

Three hundred thirteen adult suckers were captured during February–April 2007: 125 Apalachicola redhorse, 94 spotted suckers, and 94 quillback (Table 1). Apalachicola redhorse (Figure 2) and spotted suckers exhibited characteristics of reproductive condition such as full development of nuptial tubercles, loss of body mucus,



**Figure 2.** Male (a) and female (b) Apalachicola redhorse *Moxostoma* n. sp. cf. *poeциlurum* captured 15 March 2007 in the 1.5-km reach below Jim Woodruff Lock and Dam of the Apalachicola River near Chattahoochee, Florida.



**Figure 3.** von Bertalanffy growth curves fitted to back-calculated total length (TL) at age data from Apalachicola redhorse *Moxostoma n. sp. cf. poecilurum* (a), spotted sucker *Minytrema melanops* (b), and quillback *Carpioles cyprinus* (c) captured from the Apalachicola River, Florida, during February–April 2007. Solid lines denote growth curves fitted to males, and dotted lines denote growth curves fitted to females.

and expression of gametes. Male Apalachicola redhorse (Figure 2a) and spotted suckers exhibited extensive tubercle development. Only a portion of spawning quillback of both sexes exhibited nuptial tubercles; and further, some spawning adults were not tuberculate, yet expressed gametes. Sex ratios were skewed toward males in Apalachicola redhorse (5:1;  $\chi^2 \geq 29.2$ ,  $df = 1$ ,  $P < 0.0001$ ) and spotted suckers (2.6:1;  $\chi^2 = 9.9$ ,  $df = 1$ ,  $P = 0.002$ ), but approximated 1:1 in quillback ( $\chi^2 \geq 0.2$ ,  $df = 1$ ,  $P = 0.66$ ).

### Age structure and growth

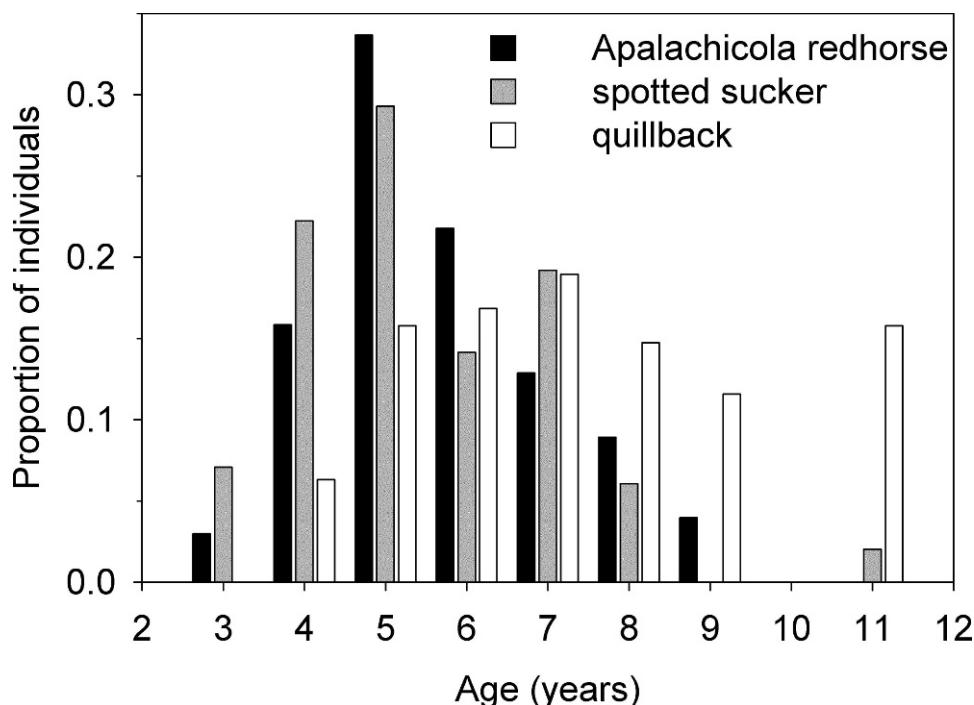
Age estimates derived from scale and otolith readings were generally in agreement for Apalachicola redhorse and spotted sucker. Scales tended to slightly overestimate the maximum age of Apalachicola redhorse (scales: 9 y; otoliths: 8 y) and spotted sucker (scales: 10 y; otoliths: 8 y). However, scales and otoliths did not provide similar age estimates for quillback. Maximum age of quillback was 17 y when from scales, and 30 y when from otoliths. Quillback ages were grossly underestimated past 10 y when using scales (Table S3, *Supplemental Material*).

Age at first maturity seems to be 3–4 y for male and female Apalachicola redhorse and spotted suckers as estimated from both dissection and the inflection of von Bertalanffy growth curves (Figure 3). Further, 73% of sexually mature Apalachicola redhorse and 72% of sexually mature spotted suckers were aged 3–6 y (Figure 4). Based on the same criteria, quillback of both sexes seem to reach age at first maturity between 4 y and 6 y of age. However, only 39% of spawning quillback were aged 4–6 y; the remainder of individuals were  $\geq 7$  y of age based upon estimates from scales (Figure 4), which resulted in an age-structure that was significantly older than that of Apalachicola redhorse and spotted sucker ( $\chi^2 \geq 35.9$ ,  $df = 7$ ,  $P < 0.0001$ ). There was no difference in the age structure of Apalachicola redhorse and spotted sucker ( $\chi^2 = 12.4$ ,  $df = 7$ ,  $P = 0.09$ ).

Length-at-age correction factors were calculated as 24 mm for spotted suckers, 29 mm for Apalachicola redhorse, and 46 mm for quillback. Sex-based differences in growth were detected in all three species ( $F \geq 5.47$ ,  $P \leq 0.001$ ) and separate von Bertalanffy growth curves were fitted for males and females within each (Table 1). Females tended to be larger than males at a given age regardless of species, and all three species grew rapidly until age 4 (Figure 3). Apalachicola redhorse was the fastest growing of the three species, reaching a mean ( $\pm$  SE) TL  $385 \pm 4$  mm after 4 y, compared with  $369 \pm 5$  mm and  $342 \pm 4$  mm TL for spotted sucker and quillback, respectively. After age 4, growth tended to slow in all three species. It is important to note that the growth curve parameters and annual growth beyond 10 y were biased by utilizing scales in quillback.

### Environmental influences on growth

Flows in Apalachicola River were highly variable over the period encompassed by the lifetimes of the catostomids used in this study (Figure 5), including several periods of higher flows and an extended drought. In all three species, higher than predicted growth seemed to be associated with a larger proportion of high-flow observations per year (Figure 6a–c;  $F_{3,619} = 15.44$ ,  $P < 0.0001$ ), though this trend was not significant for quillback ( $t_{1,619} = 0.92$ ,  $P = 0.36$ ). Years with a larger proportion of low flows were not associated with a departure from predicted growth in any of the three species ( $F_{3,623} = 1.08$ ,  $P = 0.30$ ). Increasing occurrence of extreme flows was associated with growth that was less than predicted for Apalachicola redhorse and spotted sucker, regardless of whether the flows were extreme



**Figure 4.** Age-frequency histogram comparing spawning population age-structure of Apalachicola redhorse *Moxostoma* n. sp. cf. *poecilurum*, spotted sucker *Minytrema melanops*, and quillback *Carpioles cyprinus* captured from the Apalachicola River, Florida, during February–April 2007.

high ( $Q_{10}$ :  $t_{1,619} \geq 3.51$ ,  $P \leq 0.0005$ ) or extreme low ( $Q_{90}$ : Figure 6d–f;  $t_{1,619} \leq -2.08$ ,  $P \leq 0.04$ ). Quillback growth seemed to be less sensitive to the effects of extreme flows than that of the other two species ( $t_{1,621} \geq 1.43$ ,  $P \geq 0.02$ ; Figure 6b,e). There was no meaningful difference in the response of growth to flow between Apalachicola redhorse and spotted sucker ( $F_{1,322} = 1.71$ ,  $P = 0.19$ ).

### Mortality

Estimates of  $Z$  ( $\pm$  SE) were  $0.52 \pm 0.14$  for Apalachicola redhorse,  $0.53 \pm 0.11$  for spotted sucker, and  $0.29 \pm 0.04$  for quillback. The instantaneous mortality rate of quillback was lower than that of the other catostomids ( $F_{1,14} = 5.60$ ,  $P = 0.03$ ), but there was no difference between Apalachicola redhorse and spotted sucker ( $F_{1,14} = 0.00$ ,  $P = 0.99$ ).

### Reproductive ecology

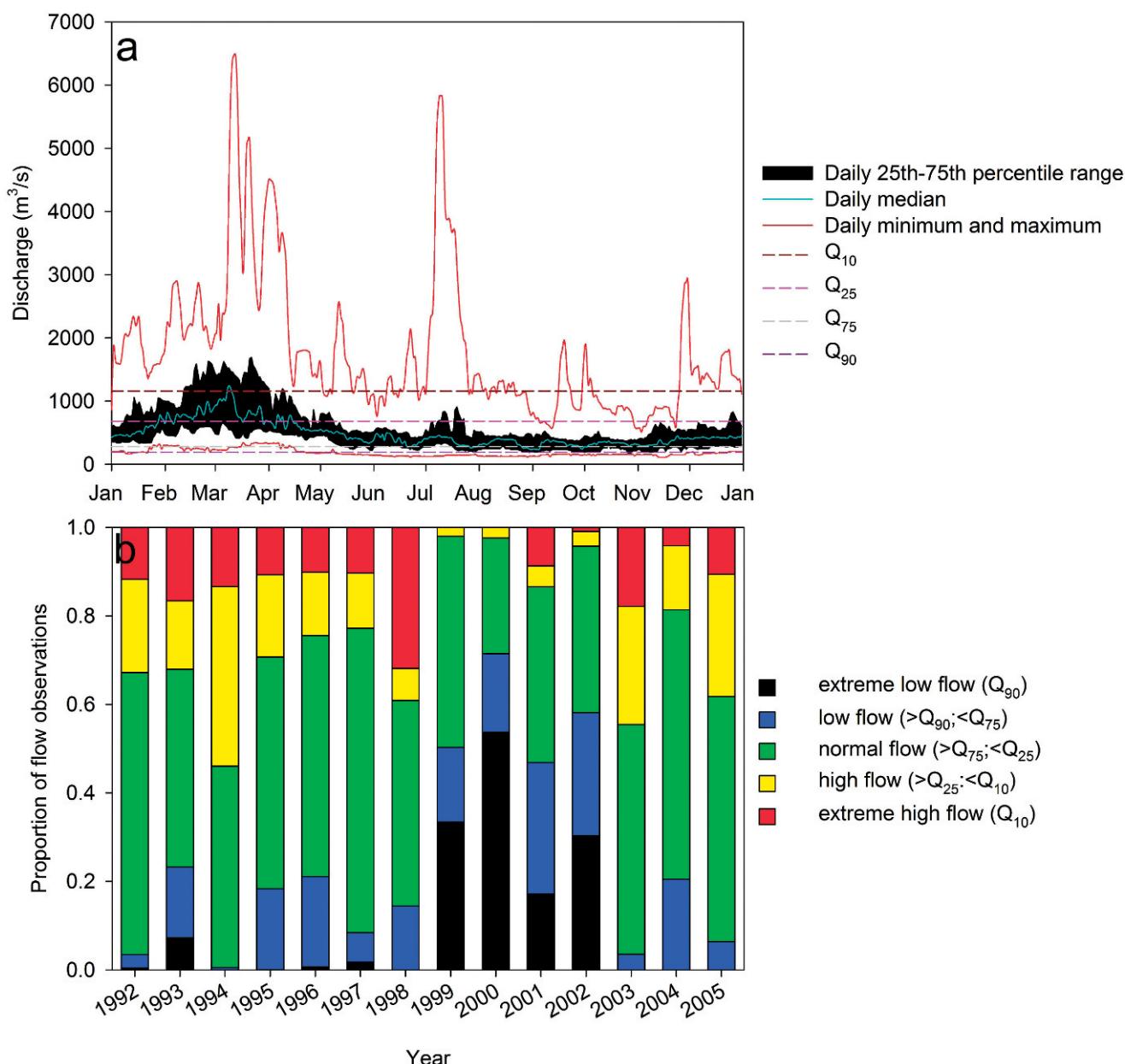
Apalachicola redhorse and spotted sucker overlapped temporally and spatially during spawning. Spotted suckers were the first species observed on the main channel gravel bars below JWLD (Figure 1). Both sexes were captured from spawning aggregations in mid-February at water temperatures of  $13^{\circ}\text{C}$ . At base flows, adults were routinely observed holding positions in the laminar flow at depths ranging from 0.5 to 2.0 m. By late February–early March at water temperatures of  $14^{\circ}\text{C}$ , adult Apalachicola redhorse of both sexes began arriving on the same gravel bars. Apalachicola redhorse exhibited extensive overlap with spotted sucker; small groups of individuals were distributed within the spotted sucker aggregation. Females of both species collected during

this time had mature, but still complete, ovaries. However by mid- to late March at water temperatures of  $18^{\circ}\text{C}$ , a portion of females of both species had partially or completely spent ovaries. By mid-April, the number of spawning adults observed on the gravel bars rapidly declined as water temperatures reached  $20^{\circ}\text{C}$ .

Quillback spawning overlapped temporally with the other two species but not spatially. Quillback were not captured or observed with the other catostomid species on the main gravel bars (Figure 1). Instead, females and males were typically captured in groups of 5–10 individuals over sand–gravel substrates on the periphery of the gravel bars or along shallow river banks. Females dominated early captures, and then both sexes were equally represented soon after. Females collected during late February–mid-March had developing ovaries. Females expressing gametes were first captured during late March and April at water temperatures of  $18$ – $20^{\circ}\text{C}$ . Few males and females were observed with nuptial tubercles in late February, but the number of adults with tubercles and/or expressing gametes increased through March and April. However, not all mature adults expressing gametes exhibited nuptial tubercles. As water temperatures approached  $20^{\circ}\text{C}$  in mid-April, the only catostomid species observed during sampling below JWLD was quillback. Finally, in late April, the number of quillback observed also declined, but did not change as drastically as the decline of observations for the other two species.

### Fecundity and egg lipid content

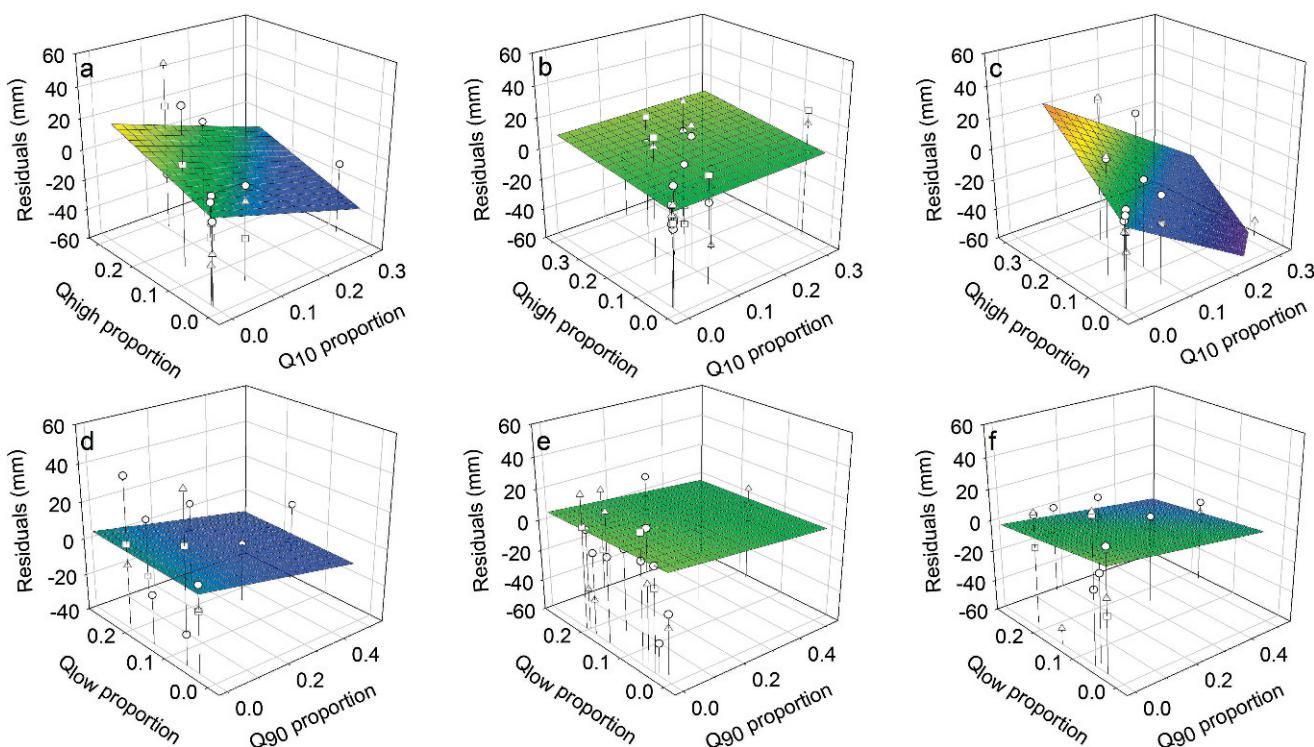
Mean fecundity of the three catostomid species differed from one another ( $F_{2,38} = 56.61$ ,  $P < 0.0001$ ;



**Figure 5.** Daily (a) and annual (b) discharge of the Apalachicola River, Florida. Daily discharge data are from 1987 to 2005 and are summarized by the median daily discharge, the 25th–75th percentile range of daily discharge, and the minimum and maximum daily discharge. Annual discharge data are from 1992 to 2005 and are summarized as proportion of observations within one of five streamflow quantiles. These streamflow quantiles are illustrated by the dashed lines on panel (a). Discharge data were collected from U.S. Geological Survey streamflow-gaging station 0235800 located near the US-90 crossing in Chattahoochee, Florida at the downstream end of our study area.

Table 2). Fecundity was positively correlated with maternal age ( $r = 0.69, P < 0.0001$ ) across the catostomid species evaluated in this study, but exhibited an inverse relationship with egg size ( $r = -0.72, P < 0.0001$ ). This relationship between fecundity and egg size meant that the differences observed among the species in fecundity were accompanied by similar differences in egg mass ( $F_{2,45} = 58.24, P < 0.0001$ ). The largest eggs were produced by the relatively low-fecundity Apalachicola redhorse, while the smallest eggs were produced by the relatively high-fecundity quillback (Table 2). Catostomid

egg mass was positively correlated to maternal length, weight, and condition ( $r \geq 0.31, P \leq 0.04$ ), but negatively correlated with maternal age ( $r = -0.40, P \geq 0.01$ ). However, these relationships were not apparent when species were analyzed separately ( $r \leq 0.42, P \geq 0.16$ ), except for positive correlations between egg mass and length ( $r = 0.68, P = 0.002$ ) and weight ( $r = 0.48, P = 0.045$ ) in quillback. Percent lipid content did not correlate to maternal age, TL, weight, or condition in any of the catostomid species examined ( $-0.18 \leq r \leq -0.04, P \geq 0.24$ ); and further, no differences were found in percent



**Figure 6.** Residuals from von Bertalanffy growth curves for the first 3 y of growth of Apalachicola redhorse *Moxostoma* n. sp. cf. *poecilurum* (a, d), quillback *Carpioles cyprinus* (b, e), and spotted sucker *Minytrema melanops* (c, f) captured from the Apalachicola River, Florida, during February–April 2007 plotted against the proportion of high-flow ( $>Q_{25}$  but  $<Q_{10}$ ) and extreme-high-flow ( $>Q_{10}$ ; panels a, c, e) observations per year and the proportion of low-flow ( $>Q_{90}$  but  $<Q_{75}$ ) and extreme-low-flow ( $Q_{10}$ ; panels b, d, f) observations per year. Individual data points represent the mean residual for a particular cohort at age 1 (○), age 2 (△), and age 3 (□).

lipid content of eggs among species ( $F_{2,38} = 1.11, P = 0.34$ ) with each species having a lipid content of approximately 11–16% (Table 2; Table S4, *Supplemental Material*).

## Discussion

There is diversity in life-history strategies among the constituent species of the Apalachicola River catostomid assemblage, similar to that described for the catostomid assemblage of the Savannah River (Grabowski et al. 2008). These differences in life-history strategies potentially alter how resources are used and might enable an assemblage of ecologically similar species to avoid competition (Winemiller and Rose 1992; Bassett 1995, 1997). These differences in life-history strategy are in stark contrast to the similarities in trophic ecology

among the species. Trophic diversification, if present, seems to be relatively minor because all three species are reported to be benthic feeders with diets composed primarily of organic detritus, algae, and benthic invertebrates (Beecher 1979, Mettee et al. 1996, Boschung and Mayden 2004). Our study suggests that life-history diversification may be an important factor in the coexistence of these three species in the Apalachicola River and provides some indication of how anthropogenic disturbances might impact their populations. Quillback were the smallest in TL at age; longest-lived with a maximum age of 30 y, similar to other long-lived catostomids (Scoppettone 1988); suffered the lowest instantaneous mortality rate; had a wider range of spawning age-classes; were the most fecund, and produced the smallest eggs. Apalachicola redhorse and spotted suckers were more similar to each other than to

**Table 2.** Mean ( $\pm$  SE) total fecundity, per-unit-body-weight fecundity, egg mass, and percent lipid composition of Apalachicola redhorse *Moxostoma* n. sp. cf. *poecilurum*, spotted sucker *Minytrema melanops*, and quillback *Carpioles cyprinus* captured from the Apalachicola River, Florida, during February–April 2007.

Species	n	Mean fecundity per individual	n	Mean fecundity per unit body weight (eggs/g)	N	Mean mass per 100 eggs (g)	n	Mean lipid composition (%)
Apalachicola redhorse	8	17,689 $\pm$ 6,050	7	12.0 $\pm$ 3.5	12	0.98 $\pm$ 0.33	11	10.9 $\pm$ 9.0
Quillback	18	52,985 $\pm$ 22,048	18	45.1 $\pm$ 10.3	18	0.25 $\pm$ 0.07	17	16.2 $\pm$ 7.2
Spotted sucker	16	30,418 $\pm$ 9,466	16	25.5 $\pm$ 4.6	16	0.58 $\pm$ 0.10	16	13.0 $\pm$ 7.6

quillback in terms of life-span, mortality rates, and reproductive biology. Apalachicola redhorse was the largest in body size; had an intermediate life span; and produced the fewest yet largest eggs. Spotted suckers were intermediate for length at age, fecundity, and egg size. Juvenile spotted sucker and Apalachicola redhorse growth also seemed to be more sensitive to flow variability and extreme flows than did quillback growth.

Our study represents the first detailed description of life-history parameters for Apalachicola redhorse, an undescribed, endemic species. Mettee et al. (1996) and Boschung and Mayden (2004) provide a broad description of some basic morphometric measures, a general distribution, and general habitats. Our results are consistent with the general information supplied for spawning period and spawning habitat. However, our results indicate a much larger adult body size ranging 375–550 mm TL and a life span of 8 y, compared with an adult size range of 254–406 mm TL and maximum life span of 6 y listed by Mettee et al. (1996) or 330–462 mm TL and a lifespan of 6 y by Boschung and Mayden (2004). However, these data may have been obtained from a subpopulation above JWLD in the smaller Chattahoochee or Flint rivers. The life-history parameters identified for the Apalachicola redhorse are similar to other *Moxostoma* spp. such as notchlip redhorse *Moxostoma collapsum* (Grabowski et al. 2008). Redhorses are typically larger fishes that exhibit intermediate to long life spans, and utilize gravel substrate for spawning (Bowman 1970; Etnier and Starnes 1993; Mettee et al. 1996; Grabowski et al. 2008). Age, growth, spawning period, spawning habitat, fecundity, and secondary sexual characteristics were also similar to other *Moxostoma* spp. (Meyer 1962; Carlander 1969; Hackney et al. 1971; Etnier and Starnes 1993; Mettee et al. 1996; Grabowski and Isely 2007; Grabowski et al. 2008). The nonspawning distribution, behavior, juvenile habitat and population size of the Apalachicola redhorse remains unknown. However, given the numerous similarities to other members of the genera and extrapolating from behavioral research of other big-river catostomids (such as razorback sucker *Xyrauchen texanus* [Tyus and Karp 1990], flannelmouth sucker *Catostomus latipinnis* [McKinney et al. 1999], greater redhorse *Moxostoma valenciennesi* [Bunt and Cooke 2001], and robust redhorse *M. robustum* [Grabowski and Isely 2006; Grabowski and Jennings 2009]), Apalachicola redhorse is likely potadromous (migrating seasonally between riverine habitats) including to the spawning grounds below JWLD.

The results for spotted sucker age, growth, and reproduction were similar to midwestern and other southern U.S. populations (Pflieger 1975; Rohde et al. 1994; Grabowski and Isely 2007; Grabowski et al. 2008), which suggests that there is little variation in life-history parameters across its wide geographic range. Until now, Gulf Coast spotted sucker populations had not been studied in depth to determine whether life-history characteristics of populations in these isolated drainages had diverged from those in other portions of the range. Age-structure of spawning adults, age at first maturity, growth rates, and spawning habitat were similar to

populations in Oklahoma, Minnesota, and South Carolina–Georgia (Carlander 1969; Pflieger 1975; Grabowski and Isely 2007; Grabowski et al. 2008). However, differential growth patterns between sexes identified herein were only noted in the Savannah River, South Carolina–Georgia, population (Grabowski et al. 2008). Spawning period, spawning habitat, and secondary sexual characteristics were similar to those reported from other southern river populations (McSwain and Gennings 1972; Mettee et al. 1996; Grabowski and Isely 2007).

Our results suggest that the Apalachicola River quillback population exhibited differences in life-history characteristics compared with those of other populations. Fecundity was less for Apalachicola River females than for the Manitoba population at equivalent body weight (Parker and Franzin 1991), but similar to populations in Iowa and Ohio. Age estimates derived from scales were similar to other populations (Woodward and Wissing 1976; Parker and Franzin 1991) and to estimates generated in the Apalachicola River in the late 1970s (Beecher 1979). However, the maximum age of 30 y has been previously reported for only one other quillback population (Parker and Franzin 1991). Our results indicate scale readings grossly underestimated quillback age after 10 y. Age underestimation from scales has been previously reported for other catostomids (Scoppettone 1988; Sylvester and Berry 2006). The maximum age for quillback based on scales has been reported as 11–13 y (Woodward and Wissing 1976; Parker and Franzin 1991), compared with 17 y in this study. As noted by Madsen (1971), sex determination of quillback should be based on gamete expression, because presence of nuptial tubercles is unreliable for this species. Both males and females had nuptial tubercles, but some mature males and females were not tuberculate. General spawning behavior and spawning habitat selection appear to be similar to that reported for other populations. Spawning aggregations in small groups of 5–10 individuals over sandy to fine gravels in various velocities has also been reported for midwestern U.S. and Canadian populations (Pflieger 1975; Curry and Spacie 1984; Parker and Franzin 1991).

Quillback seem to have evolved the strategy of a longer life span with maximum size and fecundity delayed beyond the maximum age for the other species. Also, quillback produced a high number of smaller eggs. In contrast, the larger, shorter lived Apalachicola redhorse produced fewer but larger eggs. These strategies display the reproductive trade-offs between the quantity of eggs and the size of eggs produced, which is common in teleost fishes (Kamler 1992; Wine-miller and Rose 1992, 1993; Wootton 1999). The strategy of producing large eggs is most common in freshwater demersal brood-hiders (Balon 1975; Kamler 1992; Wine-miller and Rose 1992; Wootton 1999). Both Apalachicola redhorse and spotted suckers produced significantly larger eggs and were the species observed spawning en masse on the main channel gravel bars. Spawning behavior, which entailed excavation of gravels during gamete release, was similar to other main channel



gravel-spawning catostomids (Bunt and Cooke 2001; Grabowski and Isely 2007). In contrast, quillback were not observed exhibiting this behavior and were rarely captured on the main channel gravel bars even during a limited number of night-sampling events. Quillback were captured in small groups over substrates with mixed sand–gravel substrates near littoral riverbank habitats. Quillback have been reported to be mid-water broadcast-spawners that prefer substrates with smaller particle sizes (Smith 2002), a strategy that would tend to favor high fecundity and lower parental investment per egg (Balon 1975; Kamler 1992; Winemiller and Rose 1992; Wootton 1999).

Catostomids of the Apalachicola River exhibited a number of general reproductive trends that are common among teleost fishes. Mean egg size was negatively correlated with fecundity in all three species, an evolutionary trade-off frequently exhibited by oviparous fishes (Kamler 1992). Also, fecundity among individual female quillback and spotted sucker was positively correlated with maternal age and body weight, which is a common, but not constant, characteristic of oviparous fishes (Kamler 1992; Wootton 1999). Egg weight was variable among conspecifics but did not correlate with individual length, weight, condition, or age for Apalachicola redhorse and spotted sucker, and only relatively weak correlations existed for quillback body size. Further, mean percent lipid content was similar for all three species, regardless of reproductive strategies. Percent lipid content of eggs did not correlate with maternal age, length, or weight. Percent lipid contents of eggs produced by these species were similar to values averaging 13.2% found for Savannah River catostomids (T. B. Grabowski and A. T. Fisk, unpublished data). Given that catostomids deposit eggs onto or within the substrate, we speculate that there is an upper bound on the lipid content of their eggs beyond which the eggs are no longer negatively buoyant. However, further research is needed to confirm these results because the effects of a relatively small numbers of females sampled, each likely at different stages in their spawning season, may have influenced our findings. Egg quality may exhibit considerable variation within individual fish over the course of a spawning season (for review see Brooks et al. 1997).

The observed trend in the reproductive ecology and biology of Apalachicola River catostomids may be an artifact of the different proposed evolutionary origins of these two types of catostomids. Quillback are members of an older lineage (Subfamily Ictiobinae) that is thought to have arisen in larger, higher order rivers, while redhorses and spotted suckers (Subfamily Moxostomatini) are thought to have originated in mid-order streams and secondarily invaded large river habitats (Smith 1992). The evolutionary history in different orders of lotic habitats supports findings of Winemiller and Rose (1993), which suggest that high fecundity and smaller eggs results in higher larval survival in spatially or temporally patchy environments, such as the high-order rivers thought to be inhabited by ancestral ictiobines; whereas, lower fecundity with larger eggs results in higher larval

survival in habitats that are spatially or temporally predictable in terms of resource availability, which would be characteristic of the smaller order streams and rivers thought to be inhabited by ancestral moxostomatine suckers. Furthermore, the higher current velocities characteristic of smaller order streams may have provided selection pressure for the egg burying and/or hiding behaviors seen in moxostomatine suckers, whereas a similar pressure would have been experienced by the ancestral ictiobines inhabiting large rivers with slower current velocities.

### Conservation implications

Aside from being an interesting illustration of how the evolutionary history of catostomids may have molded present day assemblages, these differences in life-history strategies among species may have implications for their management and conservation. The flow regime of the Apalachicola River has already been altered and further deviations have been predicted as human demand increases and annual precipitation becomes more variable, producing extended periods of low-flow and/or drought conditions (Gibson et al. 2005). Our results suggest that extended periods of extreme flows, particularly extreme low flows ( $\le Q_{90}$ ), may have a negative impact on the growth of juvenile catostomids, particularly Apalachicola redhorse and spotted sucker. Further, the loss of high flows (that is, flows between  $Q_{25}$  and  $Q_{10}$ ), has the potential to have detrimental effects on the growth of juvenile Apalachicola redhorse and spotted sucker. Although extreme low-flow conditions are associated with a decline in productivity and alterations in habitat availability and quality (Matthews and Marsh-Matthews 2003), our data do not provide a clear explanation as to the reason that Apalachicola redhorse and spotted sucker would be more sensitive to these conditions. These species may require habitats that cannot be accessed, such as off-channel backwaters and oxbows, or that are greatly reduced in quantity or quality, such as shoals, during periods of extreme low flows. Little is known about the habitat requirements of juvenile redhorses or spotted sucker. However, young-of-year *Carpioles* spp. have been shown to use sand bank habitats along the river edge (Beecher 1979; Peterson and Jennings 2007), and this habitat generally increases in abundance during stable, low-flow years (Peterson and Jennings 2007). The abundance of habitat during low flows may have contributed to ameliorate the effects of low flows on quillback growth. It is important to note that our results may underestimate the potential effects of flow on growth within the three species because the use of back-calculated TLs meant that we only accounted for fish that were able to grow well enough to survive these early life-history stages. For example, an alternative explanation for the observed relationships is that juvenile catostomids might suffer lower mortality rates during lower flows, and thus the reduced growth rates are a result of increased density superimposed upon diminished resources (i.e., density-dependent effects). Further, the underestimation of quillback ages from scales was likely a source of error in this analysis. A longer term



experiment that sampled juvenile age classes would be necessary to assess the full effect of flow on growth and mortality.

Gilbert (1992) reported that dam construction has already altered or eliminated much of the Apalachicola redhorse habitat. The effects of altered flow-regimes on the remaining Apalachicola redhorse population and on the other catostomid species combined with this loss of habitat may threaten the persistence of these populations. Thus, complete life-history information and ecological response of Apalachicola River fish species to flow regulation would enhance the ability to incorporate the needs of the fishery resources into future management decisions. Further, understanding the evolutionary origins of the various life-history strategies and reproductive biology of fish will aid in fisheries management and conservation. Although this study is a positive first step in providing life-history information for sucker species of the Apalachicola River, gaps still remain in the life history and ecology of the suckers, as well as other Apalachicola River fish species. Given the biogeographical context that has led to the basin supporting a substantial number of endemic species such as the Apalachicola redhorse, and high species diversity in general, continued support for basic and applied research of the Apalachicola River ecosystem is warranted.

## Supplemental Material

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

**Table S1.** Annual flow summary from 1987 to 2005 of the Apalachicola River below Jim Woodruff Lock and Dam near Chattahoochee, Florida, based on flow data collected at 15-min intervals by U.S. Geological Survey gaging station 0235800. The proportion of observations  $>1,158 \text{ m}^3\text{s}^{-1}$  ( $>Q_{10}$ ), between 682 and  $1,158 \text{ m}^3\text{s}^{-1}$  ( $Q_{\text{high}}$ ), between 280 and 682  $\text{m}^3\text{s}^{-1}$  ( $Q_{\text{normal}}$ ), between 190 and 280  $\text{m}^3\text{s}^{-1}$  ( $Q_{\text{low}}$ ), and  $<190 \text{ m}^3\text{s}^{-1}$  ( $<Q_{90}$ ) are indicated for each year.

Found at DOI: <http://dx.doi.org/10.3996/012012-JFWM-008.S1> (2 KB TXT).

**Table S2.** Daily median, 25th and 75th percentile, minimum, and maximum flow statistics for 1 January (day 1) to 31 December (day 365) during 1987–2005 for the Apalachicola River below Jim Woodruff Lock and Dam near Chattahoochee, Florida, based on flow data collected at 15-min intervals by U.S. Geological Survey gaging station 0235800.

Found at DOI: <http://dx.doi.org/10.3996/012012-JFWM-008.S2> (24 KB TXT).

**Table S3.** Total length (TL); cohort; sex; age (estimated from scales and otoliths); back-calculated age, year, and total length; and annual growth of Apalachicola redhorse (AR) *Moxostoma n. sp. cf. poecilurum*, spotted sucker (SS) *Minytrema melanops*, and quillback (QB) *Carpioles cyprinus* collected from a 1.5-km reach below Jim Woodruff Lock and Dam in the Apalachicola River near Chattahoochee, Florida, during February–April 2007.

Jim Woodruff Lock and Dam in the Apalachicola River near Chattahoochee, Florida, during February–April 2007.

Found at DOI: <http://dx.doi.org/10.3996/012012-JFWM-008.S3> (75 KB TXT).

**Table S4.** Age, total length (TL), weight (W), fecundity, mass per 100 eggs, and percent lipid content of eggs of Apalachicola redhorse (AR) *Moxostoma n. sp. cf. poecilurum*, spotted sucker (SS) *Minytrema melanops*, and quillback (QB) *Carpioles cyprinus* collected from a 1.5-km reach below Jim Woodruff Lock and Dam in the Apalachicola River near Chattahoochee, Florida, during February–April 2007.

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