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REGULAR ARTICLE

GROWTH AND LONGEVITY ESTIMATES FOR MUSSEL POPULATIONS IN THREE OUACHITA MOUNTAIN RIVERS

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ABSTRACT

Freshwater mussels are a unique guild of benthic invertebrates that are of ecological and conservation importance. Age and growth determination are essential to better understand the ecological role of mussels, and to effectively manage mussel populations. In this study, we applied dendrochronology techniques and Ford-Walford analyses to determine growth parameters of mussel species collected in three Ouachita Mountain Rivers (Kiamichi, Mountain Fork, and Little Rivers). We collected six species of mussels, *Actinonaias ligamentina*, *Amblema plicata*, *Fusconaia flava*, *Ptychobranchus occidentalis*, *Quadrula pustulosa* and *Quadrula verrucosa*, created thin sections, and analyzed the internal annuli to determine growth and longevity estimates. Annual growth was validated in 12 of the 17 populations we sampled, and the series intercorrelation for the validated populations ranged from 0.108 to 0.477. The predicted average maximum validated age was 43 years, ranging from 15 to 79 years, while the growth constant (*K*) ranged from 0.038 to 0.137. Growth and longevity were inversely related. Growth patterns were more synchronous at local sites compared to river and regional scales, suggesting that local environmental conditions likely influence growth rates. This study provides the first reported growth parameters for mussels in Ouachita Mountain rivers of southeastern Oklahoma and will be useful in understanding the life history traits of these mussel populations.

KEY WORDS - Unionoida, Life History, Age, Growth Rate, Ouachita Mountain Rivers

INTRODUCTION

Freshwater mussels (Unionoida) are a unique guild of benthic invertebrates that are ecologically important, but are of conservation concern. Ecologically, mussels contribute to the overall structure and function of stream ecosystems. As filter feeders, mussels facilitate the transformation of nutrients that benefit primary (Allen et al. 2012; Atkinson et al. 2013) and secondary production (Howard and Cuffey 2006; Allen et al. 2012; Spooner et al. 2012), and help tighten downstream nutrient spirals, which increases the overall efficiency of streams per unit area (Atkinson et al. 2013). Mussel shells also provide habitat by increasing surface area for algae and macroinvertebrate colonization (Vaughn and Hakenkamp 2001).

From a conservation standpoint, mussels are a very diverse group of species. Nearly 300 species occur in North America (Graf and Cummings 2007; Bogan 2008) but almost 70% of the species have gone extinct or are currently listed as endangered, threatened, or of special concern (Williams et al. 1993; Neves 1999). Historically, the lack of age, growth, and longevity information hindered conservation efforts (Neves et al. 1997). Recent advances in methods to determine age and growth have improved the understanding of mussel life history (Anthony et al. 2001; Rypel et al. 2008; Haag 2009; Haag 2012), but increased efforts are still needed to understand differences among species, individual populations, or geographic regions of interest.

Mussels deposit growth rings, analogous to annual growth rings in trees or fish scales and otoliths, from which age and growth data can be interpreted. Validating the rate at which mussels produce rings is critical in order to obtain accurate age and growth estimates (Beamish and McFarlane 1983). Traditional mark-recapture methods have been

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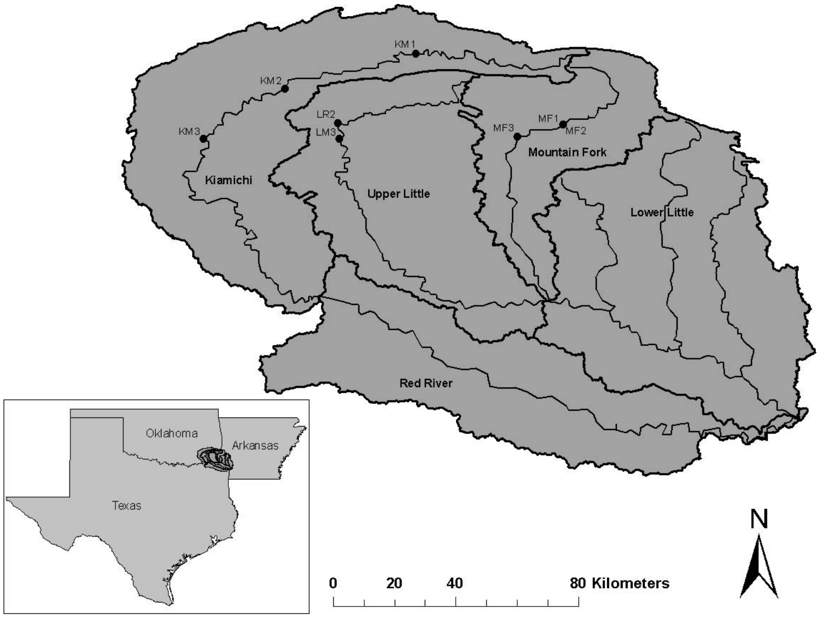

Figure 1. Regional map and locations of the eight sites where mussels were collected throughout the Kiamichi, Mountain Fork, and Little Rivers (K = Kiamichi River, L = Little River, and M = Mountain Fork River; numbers represent the site number for that specific river; M1 and M2 were too close to differentiate at this scale).

effective in validating annual ring deposition (Haag and Commens-Carson 2008), but can present bias in age and growth estimates due to handling and limited data ranges (Haag 2009). More recent approaches utilize common dendrochronological cross-dating techniques to validate ring production (Rypel et al. 2008; Haag and Rypel 2011; Sansom et al. 2013). This method, which typically uses shell thin sections to interpret growth rings, is less time intensive than mark-recapture, can result in larger sample sizes, and can also identify false or missing rings (Haag and Commens-Carson 2008). Recent advances in using this technique have improved our understanding of mussel life history (e.g. Rypel et al. 2008; Haag and Rypel 2011; Sansom et al. 2013). However, since individual populations often exhibit highly plastic growth patterns, growth often cannot be generalized within a species (Haag and Rypel 2011). Therefore, additional life history information regarding growth rates and longevity is needed from individual populations to provide meaningful management and conservation efforts at the population level (DeVries and Frie 1996; Campana and Thorrold 2001; Haag and Rypel 2011).

The aim of our study was to quantify the growth rates and variability of these rates within and across unionid freshwater mussel species in three watersheds in an understudied geographic region, the Ouachita Mountains. We applied dendrochronology techniques and Ford-Walford analyses to age and estimate growth rates of mussels, analyzed differences in growth rates within and across species, and compared our estimates to data from other regions.

METHODS

Study Sites and Shell Collection

Mussels were collected from three rivers (Kiamichi, Little, and Mountain Fork; Figure 1) during the summer of 2010 as part of a larger study (Atkinson et al. 2013; Atkinson et al. 2014). The rivers are tributaries of the Red River and share regional species pools. Headwaters and mid-reaches flow through the Ouachita Mountains ecoregion, with lower reaches flowing through the Gulf Coastal Plain ecoregion. The Ouachita Mountains ecoregion, which covers 46,500 km^2 in central Arkansas and southeastern Oklahoma (U.S.), is characterized by a sub-humid subtropical climate, mixed forests/woodlands, rugged mountains, broad valleys, and several large gravel-bed rivers (OEAT 2003). This region is a center of speciation for both terrestrial and aquatic organisms, with a large number of endemic species (Mayden 1985). Mussel diversity is noteworthy with >60 species, including 4 federally threatened or endangered species (Vaughn and Taylor 1999). Furthermore, these rivers support healthy and diverse mussel communities primarily due to relatively low anthropogenic impacts compared to other areas in the U.S. (Vaughn and Taylor 1999).

Mussels were quantitatively sampled from 8 sites across the three rivers. All sites were within the Ouachita Mountain ecoregion and were located upstream of any impoundments. We excavated 10, 0.25-m^2 quadrats randomly placed within each study site. Quadrats were excavated to a depth of 15 cm and all mussels were removed and identified to species. Five to ten individuals of the two or three most common species were

Table 1. Regression coefficients for linear regressions between shell height and shell length for each species (AL = *Actinonaias ligamentina*, AP = *Amblema plicata*, FF = *Fusconaia flava*, PO = *Ptychobranchus occidentalis*, QP = *Quadrula pustulosa*, QV = *Quadrula verrucosa*) in three rivers (K = Kiamichi, L = Little, M = Mountain Fork). Mean shell length % difference indicates the difference between the measured shell length and the predicted shell length using the regression coefficients.

Species and River	n	Intercept	Slope	R^2	Mean Shell Length % Difference
AL K	10	−14.750	1.913	0.880	3.10%
AP K	11	−8.281	1.473	0.846	3.29%
AP L	6	−19.256	1.693	0.891	5.10%
AP M	8	−12.449	1.666	0.922	2.28%
FF L	4	−7.009	1.459	0.971	2.39%
FF M	3	−114.763	4.025	0.999	0.05%
PO M	12	−4.817	2.307	0.942	1.94%
QP L	4	−14.226	1.480	0.922	1.27%
QP M	4	4.754	1.047	0.934	0.92%
QV L	7	−1.914	1.832	0.779	3.23%
QV M	2	15.703	1.844	NA	NA

collected from each site for tissue stoichiometric analyses (see Atkinson et al. 2013) and the shells of each individual were cleaned, marked, and cataloged for the purpose of this study.

Shell Preparation

Thin sections were created following standard methods for bivalves (Clark 1980; Neves and Moyer 1988). Each thin section was viewed and interpreted using a dissecting microscope by two individuals. True annuli were differentiated from non-annual rings following criteria in Haag and Commens-Carson (2008). Once the true annuli were agreed upon, we measured the annual growth increments using a linear encoder and digital readout in MeasureJ2X (Project J2X, VoorTech Consulting). Measurements, taken along the dorsoventral growth increment between the prismatic and nacreous shell layers, began at the most recent complete growth year and proceeded towards the umbone. Due to extensive erosion on and around the umbone on most of the specimens, the early growth years were not measurable. The linear portion of the shell that was eroded was measured and used to determine the shell height and length for the first observable growth ring.

Quality Control

Growth pattern analysis and quality control measures followed dendrochronological methods described in Rypel et al. (2008) and Sansom et al. (2013). In short, the program COFECHA was used to remove age-related growth variation and generate a standardized index for each individual. Averaging the standardized index for each population created a master chronology. From that, each standardized index was compared to the master chronology to detect dating errors (i.e. false or missing rings). All potential errors flagged in COFECHA were re-examined, and if measurement errors occurred, the appropriate growth increments were re-measured and COFECHA was re-run.

Growth Parameters

After the quality control measures, we characterized growth among populations using the von Bertalanffy growth equation

$$L_t = L_\infty\left(1 - e^{-K(t-t_o)}\right) \tag{1}$$

where L_t is the length (mm) at a given time (t - age in years), L_∞ is the predicted mean maximum length (mm) for the population, K is the Brody's growth constant that depicts the rate at which the organisms approaches L_∞ (mm/year), and t_o is the theoretical time in which the L=0 (Ricker 1975). The growth increments measured between the internal annuli represent a change in shell height, rather than length. Since a length value is needed, we used linear regressions, grouped by species and river, between the shell height and length of our specimens to predict shell length. On average, these predictions resulted in <3% difference compared to actual length measurements (Table 1), and thus we used the regression parameters to predict the length at time t, based on the height at time t.

Furthermore, because we could not accurately assess age due to excessive erosion that masked the early years in many of our specimens, we used Ford-Walford plots to estimate the parameters L_∞ and K of equation one (see Anthony et al. 2001; Hornbach et al. 2014). Ford-Walford plots were created by regressing L_{t+1} on L_t, and using the slope and intercept to calculate L_∞ and K as:

$$L_\infty = \left(\frac{a}{1-\beta}\right) \tag{2}$$

$$K = -\ln\beta \tag{3}$$

where a is the y-intercept and β is the slope of the linear regression from the Ford-Walford plot. After determining the growth parameters for each population, we estimated age at length for the first identifiable growth ring for each individual as,

$$t = \ln\left[\frac{L_\infty - L_t}{L_\infty}\right]/(-K) \tag{4}$$

Following quality control for each population, we rounded the age estimate from equation four to the nearest whole number, and subsequently added the number of identifiable rings to determine the age of each individual.

Finally, we compared growth parameters between individual populations within each river, as well as comparisons between species across the three rivers. We examined bivariate relationships between growth rate (K), longevity (A_{max}), and

Table 2. Population growth parameters for the six species (AL = *Actinonaias ligamentina*, AP = *Amblema plicata*, FF = *Fusconaia flava*, PO = *Ptychobranchus occidentalis*, QP = *Quadrula pustulosa*, QV = *Quadrula verrucosa*) at eight sites in three rivers (K = Kiamichi, L = Little, M = Mountain Fork).

Site and Species	n	Intercept	Slope	R^2	K	L_∞	Max Age	Series Intercorrelation*	Cubic Spline*	Growth at Increment Skew
K1 AP	4	5.092	0.954	0.992	0.048	109.608	79	0.176	22	−0.523
K2 AL	5	15.633	0.893	0.986	0.113	146.689	30	0.411	38	−0.728
K3 AL	5	11.308	0.912	0.996	0.092	128.892	52	0.335	44	−0.925
K2 AP	5	8.978	0.902	0.981	0.103	91.335	38	0.139	24	−0.642
L2 AP	3	10.982	0.872	0.987	0.137	85.855	34	0.302	8	−0.692
L3 AP	3	6.308	0.934	0.992	0.068	95.641	53	0.256	2	−0.767
M1 AP	4	7.145	0.928	0.996	0.075	98.970	63	0.230	22	−0.863
M3 AP	4	6.513	0.922	0.994	0.081	83.947	46	-	-	−0.953
L2 FF	3	5.664	0.939	0.995	0.063	92.112	29	-	-	−0.378
M1 FF	3	3.366	0.962	0.995	0.038	89.162	64	-	-	−0.088
M1 PO	3	9.772	0.899	0.983	0.106	96.754	44	0.349	2	−1.093
M2 PO	4	7.156	0.941	0.990	0.061	121.679	32	0.108	22	−0.459
M3 PO	5	6.455	0.940	0.994	0.062	107.124	36	0.164	36	−0.397
L3 QP	4	5.041	0.951	0.984	0.051	102.251	32	-	-	0.178
M3 QP	4	7.376	0.888	0.971	0.119	65.747	25	-	-	−0.830
L2 QV	3	12.488	0.900	0.979	0.105	125.444	15	0.477	2	−0.816
L3 QV	4	10.989	0.902	0.994	0.104	111.669	34	0.330	40	−1.427

*Series intercorrelation and cubic spline are only listed for those populations that were statistically significant and validated.

maximum length (L_∞) using linear regression. All variables were $\log_{10}$ transformed. Additionally, because body size can strongly influence growth parameters (Calder 1984; Bonsall 2005), we examined growth patterns and longevity to length-standardized values of K and A_{max} by regressing both $\log_{10}$ transformed variables onto $\log_{10}$ transformed L_∞ and used the residuals in a separate regression (White and Seymour 2004; Haag and Rypel 2011). All regressions were done in JMP (v12.0.1, SAS Institute Inc.).

RESULTS

Shell Preparation

We collected mussel shells from eight different sites in the three rivers. Three sites were located on the Kiamichi and Mountain Fork Rivers, each, while two sites were on the Little River (Figure 1). We analyzed growth parameters for 69 shells from six different mussel species including, *Actinonaias ligamentina*, *Amblema plicata*, *Fusconaia flava*, *Ptychobranchus occidentalis*, *Quadrula pustulosa* and *Quadrula verrucosa* (Table 2).

Shell erosion prevented a complete analysis of internal growth rings on all specimens. On average, shell erosion accounted for approximately 46% of the total shell. This pattern was consistent between all species and sites. Therefore, we assumed that the juvenile and early adult years of growth were missed in our analysis, and the growth parameters presented here only characterize growth of adult mussels.

Quality Control

Quality control resulted in the identification of potential errors among eight individuals. In seven of the individuals, COFECHA suggested the highest series intercorrelation was obtained by shifting the chronology one year backwards (i.e. the most recent annual growth ring was likely overlooked in the initial measurement). After reanalyzing each shell, we confirmed that the last growth ring was overlooked, and repeated the quality control for those populations. For the eighth individual, the shell margin was cracked and we initially estimated that eight growth years were missing by comparing ring counts on the umbo to the rings we measured. COFECHA suggested that the highest series intercorrelation was obtained by shifting the chronology four years ahead. Because we could not confirm this based on the shell cross-section, this individual was removed from the analysis.

After quality control, our cross-dating methods supported the assumption of annual ring formation in 12 of the 17 populations in our study (Table 2). Of these 12 populations, the series intercorrelations were significant and ranged from 0.108 to 0.477, indicating that growth was synchronous among individuals within their respective population (Grissino-Mayer 2001; Black et al. 2005; Rypel et al. 2008). In the five populations that were not validated, all series intercorrelations were negative and indicate growth among these populations is not synchronous. No populations of *Fusconaia flava* or *Quadrula pustulosa* were validated, while only one population of *Amblema plicata* was not validated (Table 2). Despite not being able to validate annual ring production via cross-dating within five of our populations, we continued to

Table 3. Population growth parameters summarized for the six species (AL = *Actinonaias ligamentina*, AP = *Amblema plicata*, FF = *Fusconaia flava*, PO = *Ptychobranchus occidentalis*, QP = *Quadrula pustulosa*, QV = *Quadrula verrucosa*) in each river (K = Kiamichi, L = Little, M = Mountain Fork).

River and Species	n	Intercept	Slope	R^2	K	L_∞	Max Age	Series Intercorrelation*	Cubic Spline*	Growth at Increment Skew
K AL	10	12.784	0.907	0.989	0.098	137.083	52	0.295	6	−0.774
K AP	11	7.397	0.926	0.988	0.077	99.766	79	0.080	8	−0.629
L AP	6	7.945	0.913	0.989	0.091	91.664	53	0.212	40	−0.706
M AP	8	6.172	0.936	0.995	0.066	96.462	63	0.282	70	−0.470
L FF	4	6.467	0.927	0.992	0.076	88.430	29	-	-	−0.494
M FF	3	3.366	0.962	0.995	0.038	89.162	64	-	-	−0.088
L QP	4	5.041	0.951	0.984	0.051	102.251	32	-	-	0.178
M PO	12	7.257	0.932	0.990	0.070	107.166	44	-	-	−0.586
M QP	4	7.376	0.888	0.971	0.119	65.747	25	-	-	−0.830
L QV	7	12.417	0.889	0.990	0.117	112.093	34	0.176	40	−1.231

*Series intercorrelation and cubic spline are only listed for those populations that were statistically significant and validated.

conduct the Ford-Walford plots to estimate growth parameters. Validation of annual ring formation among other species at the same sites and in the same rivers suggests that climate conditions are conducive for the deposition of yearly growth rings.

Growth Parameters

Overall, growth and longevity varied greatly across both species and rivers (Table 2 and 3, respectively). For example, the population of *Amblema plicata* from Site 2 in the Little River had the highest growth constant ($K = 0.137$) with a moderate maximum predicted age (34 years), while another population of *Amblema plicata* from Site 1 in the Kiamichi River had the highest predicted age (79 years), with a low growth constant ($K = 0.048$). The lowest growth constant occurred in the *Fusconaia flava* population at Site 1 in the Mountain Fork River, but this river also had some of the higher growth rates at Site 3 and well as site 1 for *Quadrula pustulosa* and *Ptychobranchus occidentalis*, respectively.

Furthermore, growth was inversely related to longevity, and K explained ~24% of the variation in longevity (Figure 2a). This pattern remained true when the effect of size was removed (Figure 2b). There was no significant relationship between L_∞ and K.

Finally, patterns of growth showed higher synchrony among local populations within a river rather than a species wide growth trend for an entire river. For all populations that were validated, the local populations had a higher series intercorrelation than when the species of each of the populations were combined for an entire river (Tables 2 and 3).

DISCUSSION

In this study, we provide growth parameters for six mussel species across three rivers in southeastern Oklahoma. The maximum predicted age that was validated in our sample was 79 years old, while the average maximum, validated age across all six species was 43 years, and thus indicates a relatively long-lived life for these six mussel species. Growth rates were highly variable, ranging from 0.038 to 0.137, which indicates the range of life history traits among different species. The growth parameters presented in this study are the first to be reported for any mussel species in southeastern Oklahoma. Furthermore, we are the first to provide growth estimates for two species, *Ptychobranchus occidentalis* and *Fusconaia flava* (however, no populations of *F. flava* were validated having true growth annuli).

Examining the growth parameters at a species level, the growth constants (K) and maximum predicted length (L_∞) were within the range of previously reported studies on similar species. Only one similar growth study has been done in the Ouachita Mountain ecoregion (Christian et al. 2000). The only species analyzed by both Christian et al. (2000) and our study, *Amblema plicata*, had similar K and L_∞ estimates (Christian et al. (2000): $K = 0.13$, $L_\infty = 87.02$; our study: K ranged from 0.048 to 0.137, L_∞ ranged from 83.947 to 109.608). From a broader regional context, the growth parameters in our study were typically towards the lower range compared to previously reported studies (Haag and Rypel 2011; Hornbach et al. 2014). Additionally, the inverse relationship between maximum predicted age and growth rate (Figure 2a) is consistent with previously reported bivalve studies (Bauer 1992; Haag and Rypel 2011; Hochwald 2011).

Although we are confident in our methods to achieve both K and L_∞, the distribution of our data may have contributed to a reduction in both of these values. Because shell erosion was observed for the majority of the shells we collected and processed, our growth parameters do not include estimates for the juvenile years of growth, where we would expect higher growth rates. Furthermore, Haag (2009) found that K decreased as the range of shell size decreased and left-skewed datasets greatly underestimated K. In our dataset, we had a slight left-skew of the distribution of shell length at growth ring increments (see Tables 2 and 3 for skew breakdown

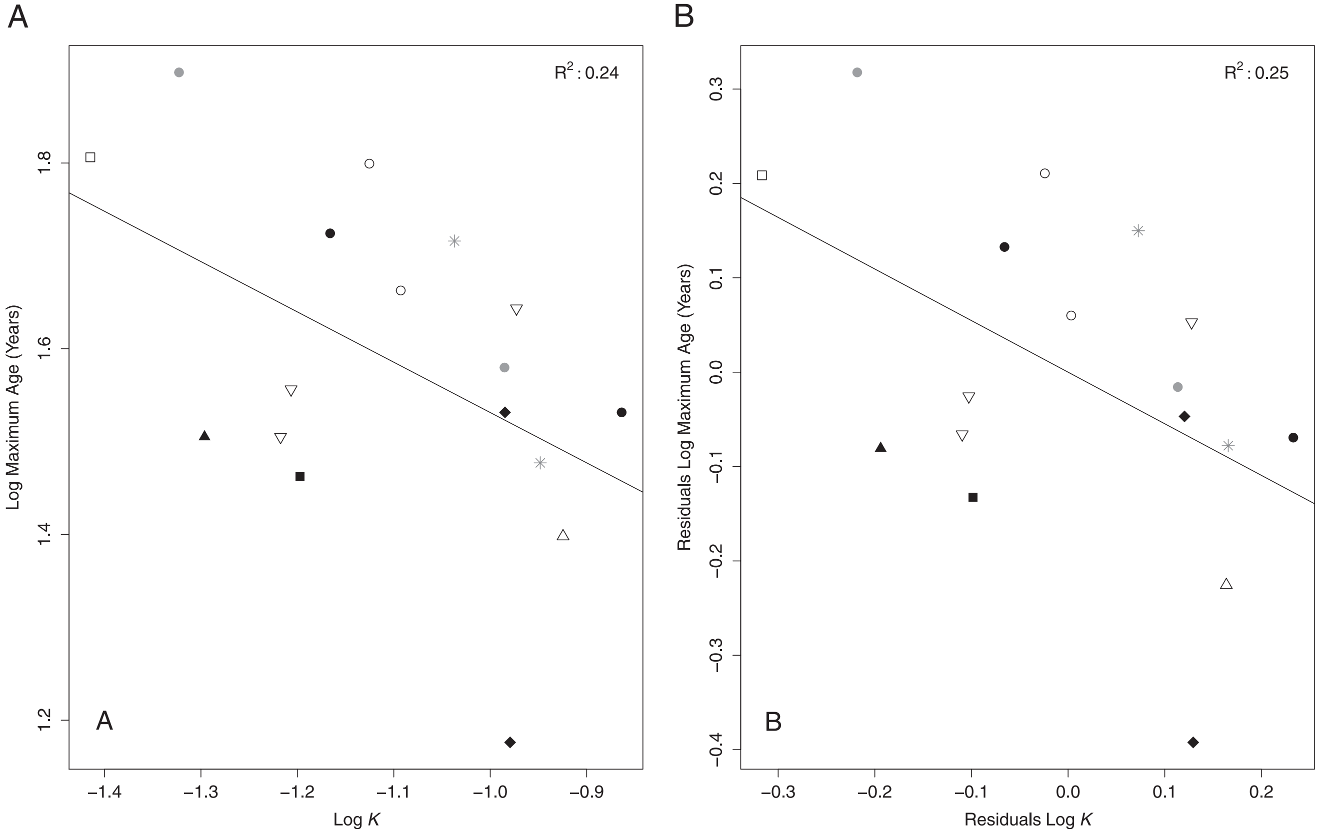

Figure 2. Mussel growth (K) and maximum predicted age (A_{max}) were inversely related (A). The growth rate (K) and maximum predicted age (A_{max}) were standardized by using the residuals of linear regressions between K and A_{max} against L_∞ to remove the effect of maximum predicted length. Regressing these residuals supported the negative relationship between maximum predicted age and growth rate (B). Rivers are differentiated by gray scale (Kiamichi River: gray symbols, Little River: black symbols, Mountain Fork River: open symbols); while mussel species are differentiated by symbols (*Actinonaias ligamentina*: ✳, *Amblema plicata*: •, *Fusconaia flava*: ■, *Ptychobranchus occidentalis*: ▼, *Quadrula pustulosa*: ▲, *Quadrula verrucosa*: ◆). Regression R^2 coefficients on both figures are for all species across all rivers.

among populations). Therefore, the combined effect of left-skew and lack of measuring juvenile growth could compensate for lower range of growth rates found in this study.

The validated age estimates (15-79 years) reported in this study are comparable to those found in Haag and Rypel (2011). It is important to note that age estimates using the von Bertalanffy growth equation have often been criticized for overestimating longevity (Haag 2009). In our study, we only used age estimates from the von Bertalanffy growth equation to predict the age at which the first observable ring was deposited. From there, we counted subsequent growth rings to obtain age estimations. This method reduced the potential for overestimating longevity throughout our dataset and removed bias in assigning an age to the first recognizable growth ring. Although on average we were only able to observe and measure growth for the latter half of the shell, the maximum predicted age of any specimen for the portion of the shell that was eroded was 11 years, and thus, our margin for error was greatly reduced.

Our approach to determine growth rates and longevity integrated dendrochronology dating techniques (Grissino-Mayer 2001; Black et al. 2005; Rypel et al. 2008) along with Ford-Walford regression plots (Anthony et al. 2001; Haag and Rypel 2011; Hornbach et al. 2014). Cross-dating allowed us to perform quality control measures on our data and identified populations with highly synchronous growth, which is indicative of regular ring formation (Grissino-Mayer 2001; Black et al. 2005; Rypel et al. 2008). While many of our specimens had large portions of eroded shells, our use of Ford-Walford plots allowed us to estimate growth rates and maximum predicted shell length for each population without having a full record of internal annuli. Furthermore, using equation four provided an unbiased age estimate to account for the portion of the shell that was eroded. Adding the subsequent, internal annuli to this age estimate provided the most accurate age estimates given large amount of erosion. When the effect of size was removed, the relationship between K and maximum age remained the same (Figure 2), suggesting that our methods to estimate growth parameters remained robust despite the shell erosion.

Overall, observed growth parameters among individuals between populations and across rivers were highly variable.

This was expected as each species likely has different life history traits (Coker et al. 1921; Stansbery 1967), and environmental conditions differ between watersheds and even local sites within a river. For example, discharge has been shown to negatively influence growth rates of freshwater mussels (Haag and Rypel 2011), and is known to strongly influence the quantity and quality of food resources (Atkinson et al. 2009), which can also impact growth rates. In our study, the higher series intercorrelations observed within local populations compared to a river scale suggest that local environmental conditions likely govern growth rates.

From a broader context, growth parameters are usually similar among species within specific tribes. Previous studies have shown that species belonging to the tribes Amblemini, Pleurobemini, and Quadrulini are typically categorized as long-lived and slow-growing (Haag and Rypel 2011). Species in the tribe Lampsilini are comparatively short-lived and fast-growing (Stansbery 1967), but can also overlap the long-lived, slow-growing tribes of Amblemini, Pluerobemini, and Quadrulini (Haag and Rypel 2011). Our results for growth and longevity at the tribe level are consistent with these documented patterns and are within the range of measurements made by Haag and Rypel (2011).

CONCLUSIONS

This study provides the first attempt to categorize growth parameters for mussel species in Ouachita Mountain rivers of southeastern Oklahoma. Growth and longevity information will be useful to understanding the life history traits of populations in southeastern Oklahoma. Using the parameters reported in this study, additional studies are in progress to assess how the growth and longevity of these mussel species are linked to environmental variables. Such studies will allow us to determine the impacts of climate change and the onset of an extended drought to the growth of these mussels, and allow us to provide better management options.

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