Freshwater Biology

WILEY

Freshwater Biology

ORIGINAL ARTICLE

Longevity, Not Stream Flow, Explains Variation in Freshwater Mussel Growth Rates Across Four Rivers

Ian A. Brunetz | Jonathan W. Lopez | Garrett W. Hopper | Irene Sánchez González | Carla L. Atkinson

Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama, USA

Correspondence: Ian A. Brunetz (iabrunetz@crimson.ua.edu)

Received: 25 July 2024 | **Revised:** 24 October 2024 | **Accepted:** 11 December 2024

Funding: This study was funded by NSF DEB-1831512 to CLA. Native mussels were collected under USFWS permit #TE68616B-1 and ALCDNR permit #2020097718468680 and permit #2016077745468680 issued to CLA. We thank F Andrus for assistance with shell sectioning. We also thank the many individuals who assisted with field sampling during mussel surveys, and two anonymous reviewers for helpful comments that improved the manuscript.

Keywords: conservation | dendrochronology | ecohydrology | life history theory | sclerochronology

ABSTRACT

1. Freshwater mussels (Bivalvia: Unionida) are among the most imperilled freshwater taxa. Yet, there is a lack of basic life history information for mussels, including data on their growth and longevity. These data help inform conservation efforts, as they can indicate whether species or populations may be vulnerable to decline and inform which species may be best adapted to certain habitats. We aimed to quantify growth and longevity in five mussel species from four river systems in the southeastern United States and test whether growth was related to stream flow. We also interpreted our findings in the context of life history theory.
2. To model mussel growth and longevity, we cut radial thick sections from the shells of mussels and used high-resolution photography to image the shells. We identified annual growth rings (annuli) and used von Bertalanffy growth models to estimate growth rate (K) and maximum age (A_{max}) across 13 mussel populations. We then used biochronological methods to remove age-related variation in annual growth in each shell. We tested whether annual growth was correlated with stream flow using discharge-based statistics.
3. We found substantial variation in K and A_{max} among species and among populations of the same species. K was negatively related to A_{max}. We did not find consistent correlations between annual growth and stream flow.
4. Our estimates of K and A_{max} align with previous studies on closely related species and populations. They also match the eco-evolutionary prediction that growth rate and longevity are negatively related. Life history theory predicts that short-lived species with higher growth rates should be better adapted to environments with cyclical disturbance regimes, whereas longer-lived species with low growth rates should be better adapted to stable environments. The lack of correlation between annual growth and stream flow suggests that mussel growth may be limited by other factors in our study system.
5. While some species seem to have relatively narrow ranges for growth and longevity, other species show wide variation among populations. This highlights the need for species- and population-specific conservation efforts. Fundamental life history information can be integrated with other species traits to predict how freshwater taxa may respond to ecological threats.

https://doi.org/10.1111/fwb.14373

1 | Introduction

Human impacts, such as alterations to hydrologic cycles by impoundments, land use, and climate change, increasingly threaten freshwater species and ecosystems (Strayer and Dudgeon 2010; Reid et al. 2019). Freshwater mussels comprise some of the most imperilled taxa (Bivalvia: Unionida; hereafter "mussels"), with 45% of species classified as near-threatened, threatened, or extinct (Lopes-Lima et al. 2018; Böhm et al. 2021). Mussels are globally distributed and contribute valuable ecosystem services such as nutrient cycling and biofiltration (Graf and Cummings 2021; Atkinson et al. 2023). As such, many conservation initiatives have begun to focus on mussels (Freshwater Mollusk Conservation Society 2016; Blevins et al. 2019; Bleasdale et al. 2020). However, a lack of comprehensive life history data for many mussel species hinders conservation efforts (Haag 2012; Moore et al. 2021; Hopper et al. 2023). Fundamental information about the growth and longevity of imperilled taxa is critical because these types of data inform when and where conservation efforts can be directed most effectively (Sæther et al. 1996). For example, in long-lived species, low growth and low recruitment of juveniles may serve as early indicators of impending declines, even before those declines are realised in adults (Haag et al. 2019, 2024).

Broadly speaking, mussels are slow-growing and long-lived (Strayer et al. 2004). However, mussels still exhibit substantial variation in growth and longevity (4 to ~200 years) (Haag and Rypel 2011; Haag 2012; Moore et al. 2021; Hopper et al. 2023). Generally, an organism's growth rate—the rate at which it approaches its maximum size—and its longevity are inversely correlated because allocating energy to rapid growth is linked to negative long-term physiological consequences, which leads to shorter individual lifespans (Metcalfe 2003). Over the long term, trade-offs between individual growth and longevity manifest at the population and community levels. When resources are limiting, slower-growing, longer-lived organisms may attain higher reproductive fitness and achieve higher abundances as a result. On the other hand, rapid growth is adaptive when extrinsic mortality is high (e.g., due to environmental disturbance) because early maturity should increase fitness and thereby abundance (Metcalfe 2003). Thus, life history traits can be used to predict the habitat conditions to which a given species is best adapted.

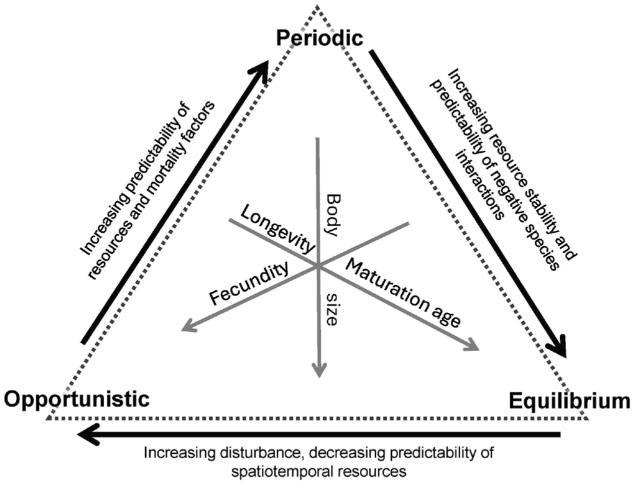

FIGURE 1 | Illustration of the freshwater mussel trilateral Life History Strategy continuum model proposed by Haag (2012). The model is originally adapted from Winemiller and Rose (1992) who proposed a similar model for fishes.

Species or populations with different life history traits inherently require different conservation and management strategies. In mussels, interspecific patterns of variation in life history traits can be classified using a trilateral continuum with three categorical endpoints that represent distinct life history strategies: equilibrium, periodic, and opportunistic strategists (Figure 1) (Haag 2012). Longevity and age at maturity are key components of the life history strategy continuum, along with fecundity and larval and adult body sizes. In the present study, we focus on longevity and growth rate—as a proxy for age at maturity. Equilibrium strategists are characterised by long life spans (> 25 years) and low to moderate growth rates, which lead to higher ages at maturity (> 3 years). Consequently, equilibrium strategists should be best adapted to stable habitats with low hydrologic disturbance frequencies. Opportunistic species typically have short life spans (≤ 10 years), high growth rates, and early maturity (0–2 years), and are thought to be adapted to habitats that are subject to frequent disturbance and instability. Periodic strategists have intermediate life spans (8–30 years), growth rates, and ages at maturity (1–3 years), which should be adapted for habitats with large-scale, cyclical disturbance regimes. Within species, growth rates and longevity may vary due to environmental factors such as temperature, land use, available food resources, and stream flow (Rypel, Haag, and Findlay 2008; Haag and Rypel 2011; Hornbach et al. 2021; DuBose et al. 2022).

Mussel growth and longevity can be quantified by studying annual growth rings, known as annuli, which are deposited within the shell when growth ceases during the winter—similar to annual growth rings in trees. Using a cross-section from a valve of a deceased mussel shell, the annuli can be counted to determine the age of the individual at death. This further allows its growth rate to be estimated mathematically at the individual, population, or species level (Haag and Commens-Carson 2008). The data from annuli also enable the construction of biochronologies, which are long-term records of annual growth that can be correlated to environmental conditions over time (Rypel, Haag, and Findlay 2009). Previous biochronological analyses suggest that correlations between stream flow and annual growth in mussels are common (Rypel, Haag, and Findlay 2008, 2009; Black et al. 2015; Brewer, Grossman, and Randklev 2024). Periods of extreme high and low flow may be especially important to individual mussel growth as they can induce stress on the animal (Rypel, Haag, and Findlay 2009). High flows are likely to cause stress to individuals if they dislodge mussels from the substrate (Gates, Vaughn, and Julian 2015; Lopez and Vaughn 2021), low flows on the other hand may induce thermal stress and hypoxia (Gagnon et al. 2004; Haney, Abdelrahman, and Stoeckel 2020). Such disturbances can decrease annual growth (Haag and Commens-Carson 2008). As such, mussel growth rates can be studied to make inferences about how mussels may respond to changing hydrologic conditions that occur in association with global climate change.

The southeastern US is a freshwater biodiversity hotspot with a rich freshwater mussel fauna, but this region is also expected to experience increases in hydrologic variability and local extinction rates in the coming decades (Spooner et al. 2011; Elkins et al. 2019; Graf and Cummings 2021; IPCC 2023). In this study, we first tested whether mussel growth varied among species and populations in four southeastern US rivers and whether growth rate was associated with longevity. We hypothesised (1) that growth rate and maximum body size differ between rivers due to underlying environmental differences, and (2) that growth rate and maximum age are negatively related due to the ecological trade-offs between growth and longevity. We interpret these hypotheses in the context of the life history strategy framework (Haag 2012). We also tested whether annual growth in mussels is correlated with stream flow. We hypothesised that (3) annual growth is correlated with annual discharge summary statistics due to the disruptions in growth caused by stressful hydrologic conditions.

2 | Methods

2.1 | Study Sites and Species

In 2018–2020, we conducted quantitative surveys of mussel aggregations at a series of sites across multiple rivers in both the Tennessee and the Mobile basins (Hopper et al. 2021; Bucholz et al. 2023). During the surveys, we collected 3–6 live individuals from five mussel species at five sites across four rivers ($N = 59$ individuals) to test the hypotheses that mussel growth parameters differ between species and sites and that growth parameters vary with streamflow (Figure 2; Table 1). We used relatively

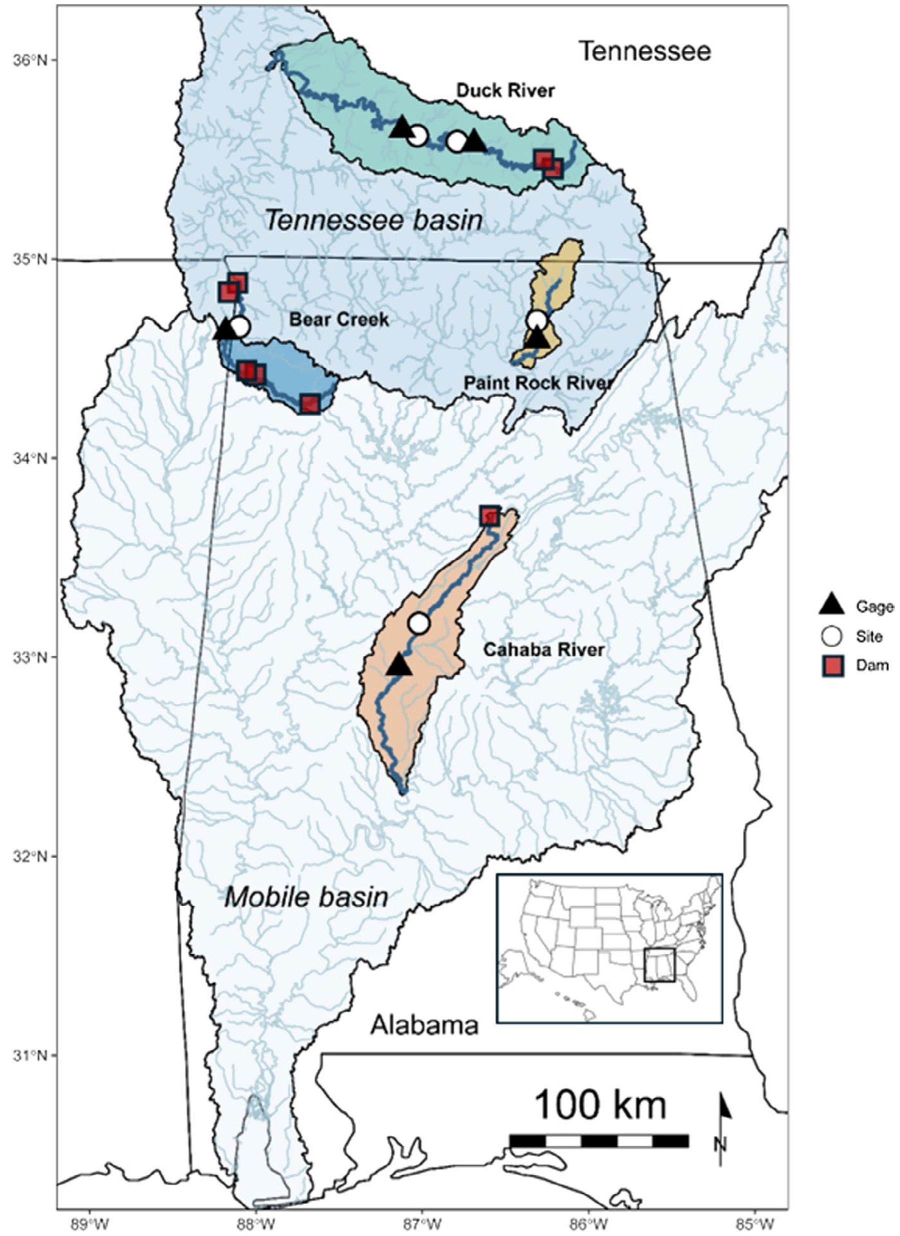

FIGURE 2 | Map of the study region. Map displays site locations (white circles), USGS stream gages that were used for stream flow calculations (black triangles), and the location of dams in each catchment (red rectangles), as well as a map of the study location in the continental USA.

TABLE 1 | Study basins and rivers, stream gages, and species identities sampled for each river.

Basin	River	Stream gage (ID)	Years of flow record	Years of flow record analysed
Mobile	Cahaba River	Centreville, AL (02424000)	1995–2024	2006–2019
Tennessee	Bear Creek	Bishop, AL (03592500)	2015–2024	2015–2018
	Duck River—Site 1	Milltown, TN (03599240)	2004–2024	2006–2019
	Duck River—Site 2	Columbia, TN (03599500)	1992–2024	1992–2019
	Paint Rock	Woodville, AL (03574500)	1995–2024	1995–2017

Note: Species came from one site in each river, except the Duck River, where species came from two sites. Also includes the years of flow record for each gage and the years analysed when testing for correlations between stream flow and annual growth.

small sample sizes because we were often limited by the number of individuals of each species that were found during a given survey, and we sought to limit the number of individuals that were euthanised from healthy populations. These small sample sizes are still considered adequate for modelling population growth responses in mussels (Rypel, Haag, and Findlay 2008; Haag and Rypel 2011).

We chose the study species *Amblema plicata*, *Cambarunio taeniatus*, *Cyclonaias tuberculata*, *Lampsilis ovata*, and *Pustulosa pustulosa* (Freshwater Mollusk Conservation Society 2023; Neemuchwala et al. 2023). These species are native to the southeastern US, and studies of other populations or closely related species suggest that growth and longevity of these species should vary across much of the known range of growth and longevity for mussels (Haag and Rypel 2011). They also represent a cross-section of mussel phylogenetic diversity, with representatives belonging to three of the major phylogenetic tribes found in North America: Amblemini (*A. plicata*); Lampsilini (*L. ovata*, *C. taeniatus*); and Quadrulini (*C. tuberculata*, *P. pustulosa*) (Graf and Cummings 2021). The study species also represent a cross-section of all mussel life history strategies—*A. plicata* can be characterised as either equilibrium or periodic strategist depending on the population, *C. tuberculata* and *P. pustulosa* are considered equilibrium strategists, and most lampsilines are thought to be periodic or opportunistic strategists—although neither *L. ovata* nor *C. taeniatus* has previously been classified using this framework (Haag 2012; Moore et al. 2021). We measured the height of each mussel along the dorsoventral axis to the nearest mm. In the Tennessee Basin, we collected mussels from Bear Creek (drainage area = 2450 km^2), the Paint Rock River (1191 km^2), and the Duck River (8100 km^2), which are tributaries of the Tennessee River. In the Mobile Basin, we collected mussels from the Cahaba River (4800 km^2), which is a tributary of the Alabama River. For sexually dimorphic species (*L. ovata* and *C. taeniatus*), we collected both male and female mussels and pooled them for further analysis because we did not always have enough individuals of both sexes to adequately assess differences among sexes (Haag and Rypel 2011).

2.2 | Shell Sectioning and Imaging

We prepared radial shell sections using modified methods for the preparation of freshwater mussel thick sections described in Haag and Commens-Carson (2008). We selected one valve from each mussel shell to cut in half along a dorsoventral plane from the umbo to the ventral margin of each individual using a petrographic trim saw (SF-8, Hillquist Inc., Arvada, CO, USA). We then mounted one of the resulting halves to a glass microscope slide using a standard mounting adhesive (Cystalbond 509, Electron Microscopy Services, Hartfield, PA, USA). We used a precision sectioning saw (IsoMet Plus, Bueler Ltd., Lake Bluff, IL, USA) to cut thick sections of ~2–3 mm from each mounted shell. After cutting was complete, we used a series of progressively finer grit sanding solutions to polish the shell surfaces.

After polishing, we took high-resolution photographs using a Canon EOS 7D Mark II camera with an EF 100 mm f/2.8 L Macro IS USM lens (Canon USA Inc., Melville, NY, USA), and four Thinklite TT685 camera flashes (Godox, Next 77 Ltd., Krakow, Poland). We used a Stackshot 3X controller (Cognisys Inc., Traverse City, MI, USA) to adjust the height of the camera on the stand to take 25 photos with different depths of focus. Then we used the focus stacking software Zerene Stacker (Zerene Systems LLC, Richland, WA, USA) to stack the photos into one high-resolution image. For this image, we edited the contrast, exposure, highlights, shadows, whites, blacks, texture, and clarity as needed in Adobe Photoshop Lightroom Classic to make the annuli stand out.

2.3 | Interpretation and Measurement of Growth Rings

We interpreted images of shell thick sections using the criteria described in Haag and Commens-Carson (2008). To distinguish between annual growth rings (true annuli), and rings formed in association with environmental disturbances to growth (disturbance rings), each image was initially interpreted by two independent observers. Annuli tend to be more diffuse and are continuous throughout the interior of the shell, whereas disturbance rings have a sharper appearance and are associated with discontinuities in the shells' prismatic layer (Haag and Commens-Carson 2008). Each observer used Adobe Photoshop to mark the locations of annuli in each shell. The two observers reviewed any discrepancies in the marked-up images until they reached an initial consensus. After reaching the initial consensus, a third observer reviewed each marked-up image and reached a consensus with the first two observers. Thus, each shell section was interpreted and agreed upon by at least three observers using consistent criteria.

To measure annual growth increments between years, we used the R package *RfishBC* (Ogle 2022). *RfishBC* is designed to collect measurements from calcified structures (originally fish otoliths) and back-calculate the estimated size of the structure at previous points in time. Briefly, we used *RfishBC* to import the marked-up versions of our high-resolution shell section photographs and marked the location of each annulus sequentially on each shell. We used the Dahl-Lea model (Lea 1910) to back-calculate the estimated height of the mussel at each putative annulus (function *backCalc*). We estimated height-at-age instead of length-at-age because we used dorsoventral cross-sections and shell dimensions including height, length, and width that are highly correlated within mussel species (Aldridge 1999).

2.4 | Quality Control and Standardisation of Growth Patterns

After we estimated height-at-age, we followed Rypel, Haag, and Findlay (2008) to quality control check putative annuli by cross-dating a standardised time series of height-at-age data across each population. We calculated growth increments as the difference between the back-calculated height-at-age values for each consecutive year across the time series for each mussel. We then used the programme COFECHA to conduct cross-dating (Holmes 1983). COFECHA uses a flexible cubic spline to remove age-related variation in growth and generate a master chronology of annual growth indices for each time series in a population (Cook and Peters 1981; Grissino-Mayer 2001). The programme then identifies potential dating errors by lagging each series forward and backward in time and comparing the correlation coefficients between each series and the master chronology at each point in time. We used a custom programme written by DuBose et al. (2022) to fit a range of initial spline flexibilities from 1–50 to maximise the initial inter-series correlation coefficients for each population (Black, Boehlert, and Yoklavich 2005; Rypel, Haag, and Findlay 2008) (Table 2). When COFECHA indicated that lagging a series 1–3 years would improve the inter-series correlation, we checked for interpretative errors in the corresponding shell section for that series, corrected the photograph, and repeated the back-calculation steps. If no clear interpretative errors were found, we retained the unmodified photograph in the data set. Following the quality control procedure, we re-ran COFECHA to

TABLE 2 | Cross-dating statistics showing results of the quality control procedure.

River	Species	*n*	Initial spline flexibility	Initial inter-series correlation (*r*)	Final spline flexibility	Final inter-series correlation (*r*)	Time series
Bear Creek	*Amblema plicata*	4	35	0.326	35	0.374	1988–2018
	Cyclonaias tuberculata	3	10	0.352	10	0.662	1987–2018
	Lampsilis ovata	7	17	0.393	17	0.640	2004–2018
	Pustulosa pustulosa	5	27	0.400	25	0.472	1999–2018
Cahaba River	*Amblema plicata*	3	18	0.388	18	0.573	2006–2019
Duck River	*Amblema plicata*	3	11	0.332	10	0.745	1999–2019
	Cambarunio taeniatus	5	14	0.374	13	0.563	2006–2019
	Cyclonaias tuberculata	5	3	0.352	3	0.352	1998–2019
	Pustulosa pustulosa	5	12	0.407	22	0.445	1988–2019
Paint Rock	*Amblema plicata*	4	18	0.034	14	0.419	1998–2017
	Cyclonaias tuberculata	5	6	0.336	5	0.394	1983–2017
	Lampsilis ovata	5	19	0.482	23	0.617	2001–2017
	Pustulosa pustulosa	5	1	0.259	1	0.423	1996–2017

Note: Time series ranges do not include the year of sampling because the year of sampling does not represent a complete year of growth. All final inter-series correlations are significant at $\alpha = 0.01$ (Grissino-Mayer 2001).

determine the final optimal spline flexibility and maximise the final inter-series correlation for each population (Table 2).

Once all populations were cross dated, we detrended the corrected growth increment data to generate a standardised chronology using the R package *dplR* (Bunn 2008, 2010; Bunn et al. 2023). We used a modified negative exponential model of biological growth to remove age-related variation in growth from each series while retaining potential climatic signals in growth (Fritts 1976; Rypel, Haag, and Findlay 2008):

$$y_t = ae^{bt} + k,$$

where a, b, and k are parameters specific to each curve; a is the y-intercept, b is the rate at which the exponential curve approaches its asymptote, and k is the asymptote. The value of y_t represents expected growth at year t, and e is the base of natural logarithms. We constrained the function so that $a \geq 0$, $b \leq 0$, and $k \geq 0$ to ensure the curve took a biologically sensible form.

We then derived the observed growth values for each year and divided them by the predicted y_t values from the curve, thus deriving a standardised growth index where values > 1 represent greater than expected growth and values < 1 represent lower than expected growth. We were unable to detrend 3 of the 59 specimen time series because they were too short in duration (2–6 years) to fit the modified exponential curve. We excluded these series from further biochronological analyses, but we retained their height-at-age data.

2.5 | Data Analysis

2.5.1 | Mussel Growth and Longevity

We used the von Bertalanffy growth model (VBGM) to estimate mussel growth parameters (Haag and Rypel 2011):

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

where L_t is height-at-age t, L_∞ is the predicted mean maximum shell height of the population, K is the growth rate constant for the population, t is age in years, and t_0 is the hypothetical age at which height = 0.

We did not have a sufficient number of populations to calculate means and variances for all species' parameter estimates, so we tested for differences in K between both conspecific populations in different rivers and between populations of different species within the same river based on 95% confidence intervals. For example, if the 95% CI around the estimate of K for *A. plicata* in the one river did not overlap the 95% CI around K for *A. plicata* in a different river, we considered *A. plicata* to have different growth rates between the two rivers.

To test whether longevity was related to growth rate, we assessed whether the maximum estimated age in each population ($A_{\max}$) was related to: the growth rate constants from their respective VBGM using ordinary least-squares regression. We log transformed $A_{\max}$ and K to meet linear model assumptions of homogeneity of variance and normal distributions of residuals.

Mussels are ectotherms and therefore their growth and longevity may be impacted by temperature. Species that are native to the southeastern USA typically do not grow during time periods when the water temperatures are below ~20°C (*personal communication*, P. Johnson, Alabama Aquatic Biodiversity Center). Therefore, we used temperature data collected by HOBO water level and conductivity loggers (U20L-02 and U24-001, Onset Computer Corporation, Bourne, MA, USA) that were deployed at varying intervals between 2018 and 2021 in each study river as part of related survey efforts (Hopper et al. 2021; Bucholz et al. 2023). We determined the number of growing degree days, and the probable growing season based on mean daily temperatures over the deployment period. For each river, we calculated growing degree days using the formula:

$$\text{GDD} = \frac{T_{\max} + T_{\min}}{2} - T_{\text{base}}$$

where $T_{\max}$ = the maximum daily temperature, $T_{\min}$ = the minimum daily temperature, and T_{base} = 20°C. Then, we determined the growing season duration by calculating which day in the spring that water temperatures first increased above 20°C and which day in the autumn that temperatures decreased below 20°C.

2.5.2 | Relationships Between Growth Rate and Stream Flow

To test for potential relationships between growth rates and stream flow, we calculated hydrologic statistics using data from the United States Geological Survey's stream gage network (Table 1). For each gage, we calculated mean and median annual discharge, and coefficient of variation in discharge. As such, we truncated the flow data sets so that only data from May–October were included and recalculated mean and median annual growing season discharge, and coefficient of variation. We also used flow duration curves for each gage to calculate the number of days in each year and the respective growing seasons that mean daily flow exceeded the 90th percentile of the curve (high discharge days), and the number of days that mean daily flow was below the 10th percentile (low discharge days).

We then used Spearman correlation tests to check whether a monotonic correlation existed between each flow statistic and the standardised growth index values across the period of record. The period of record corresponded to either that of the stream gage itself, or the length of the growth chronology for the mussel population being tested, whichever was shorter.

3 | Results

3.1 | Mussel Growth Rates Vary Among Populations and Species

We successfully fit a VBGM to each mussel population based on height-at-age data derived from shell thick sections

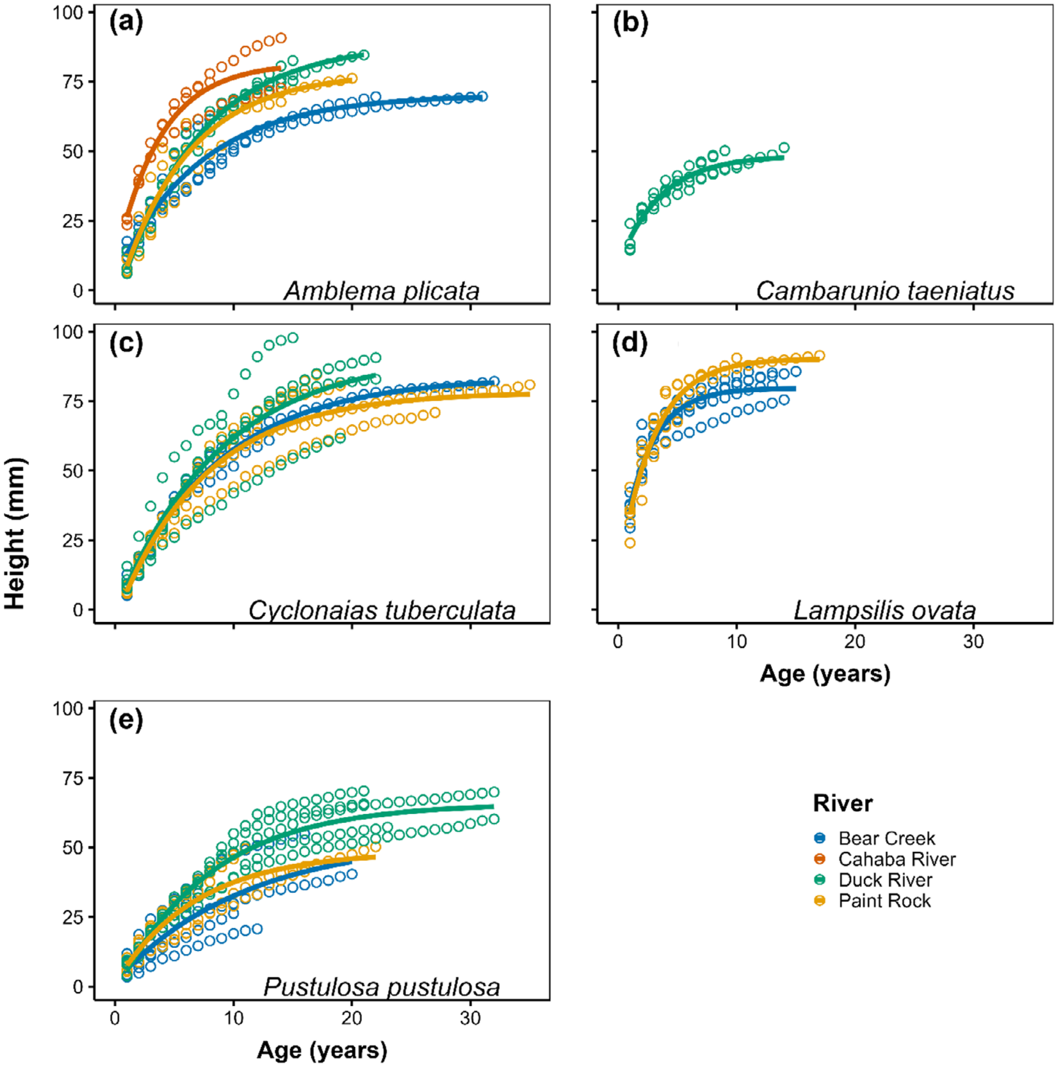

FIGURE 3 | Von Bertalanffy growth model curves for each study population. Points represent the length of an individual mussel at a given age, with lines representing the average length at the age curve of the population. Different colours correspond to different study rivers. The Von Bertalanffy growth model curves are separated by species: (a) *Amblema plicata*, (b) *Cambarunio taeniatus*, (c) *Cyclonaias tuberculata*, (d) *Lampsilis ovata*, (e) *Pustulosa pustulosa*.

(Figure 3; Table S1). The 95% confidence intervals around the resulting VBGM parameter estimates indicated that *K* varied among conspecific mussel populations from different rivers, and among species within rivers (Figure 4; Table S1). *K* was consistently high in *L. ovata* populations (range = 0.344–0.410) and *C. taeniatus* (0.279), consistently low in *C. tuberculata* populations (0.113–0.133), and relatively variable among populations of *A. plicata* (0.140–0.262) and *P. pustulosa* (0.092–0.145) (Figure 4).

3.2 | Maximum Age Decreases With Growth Rate

The highest observed A_{max} values we recorded were from *C. tuberculata* (22–35 years; Figure 3; Table S1). *Amblema plicata* (14–31 years) and *P. pustulosa* (20–32) had similar A_{max} ranges, although *A. plicata* was more variable (Figure 3; Table S1). *Cambarunio taeniatus* (14 years) and *L. ovata* (15–17 years) had lower A_{max} values (Figure 3; Table S1). A_{max} had a negative log–log relationship with *K* across all populations ($F_{1,11} = 11.9$, $p = 0.005$, $\log A_{max} = 2.2–0.5 \log K$, $R^2 = 0.52$; Figure 5).

3.3 | Growing Degree Days and Growing Season Duration Vary Among Streams

The number of growing degrees was lowest in the Paint Rock (667°C days), highest in the Cahaba River (951°C days), and intermediate in Bear Creek (844°C days) and the Duck River (810°C days). Similarly, the growing season was shortest in the Paint Rock (152 days; 17 May–16 October), longest in the Cahaba River (184 days; 28 April–29 October), and intermediate in Bear Creek (162 days; 3 May–12 October) and the Duck River (161 days; 4 May–12 October). Within species, growing degree days and growing season duration did not co-occur in systems with higher growth rates (Figure 4). For example, growth rates for *A. plicata*—the only species we sampled in all four study rivers—were statistically indistinguishable between the Cahaba River and the Paint Rock.

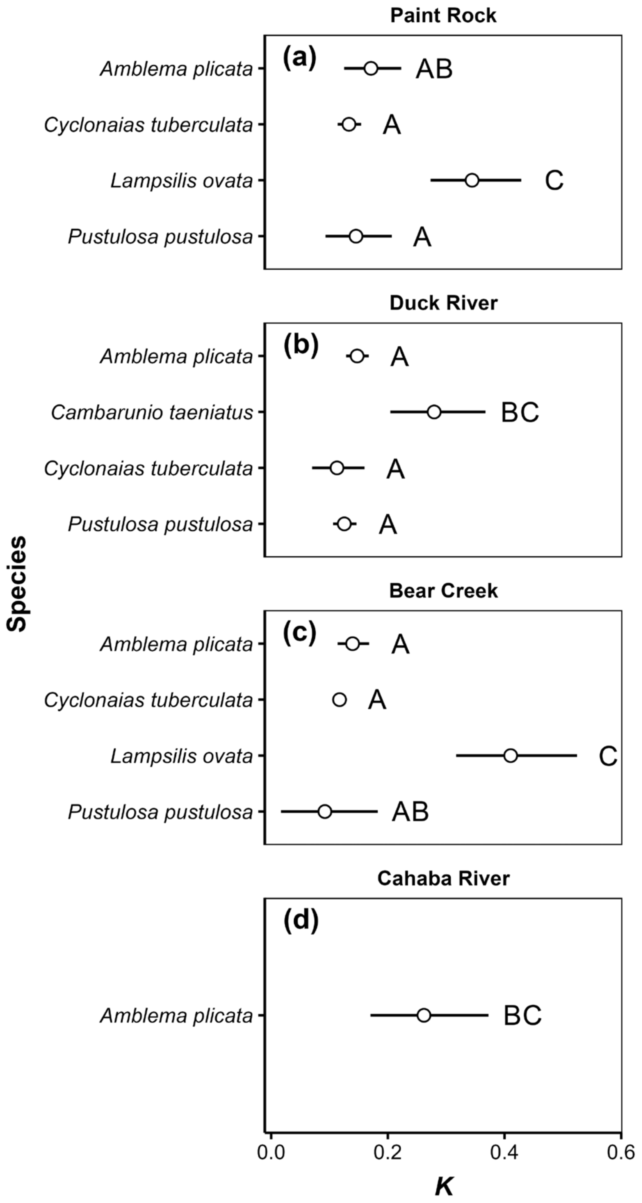

FIGURE 4 | Coefficient plots showing the point estimates of the von Bertalanffy growth constant (K) for each study population. Error bars represent 95% confidence intervals of the estimates. Letters to the right of the error bars represent differences among groups, where groups that share a common letter have overlapping confidence intervals and groups that do not share a letter are different from one another. The plots are separated by the rivers with species denoted on the y-axis. The letters distinguish which river the growth constants were taken from: (a) Paint Rock, (b) Duck River, (c) Bear Creek, and (d) Cahaba River.

3.4 | Stream Flow Was Rarely Correlated With Annual Growth

Mean growth chronologies for each population showed a similar long-term pattern characterised by alternating periods of high and low growth (Figure 6). However, when we used standardised growth indices derived from the chronologies to quantify annual growth within populations, we did not find any consistent correlations between stream flow and annual growth. Of 7 significant correlations between annual growth and stream flow, 5 occurred in the Paint Rock (Table 3). Mean correlation coefficients tended to be low (Table 3). Among mean correlation coefficients, the largest negative values were associated with annual flow statistics (number of high and low days and the coefficient of variation), while the largest positive values were associated with growing season statistics (mean and median discharge, number of low discharge days) (Table 3).

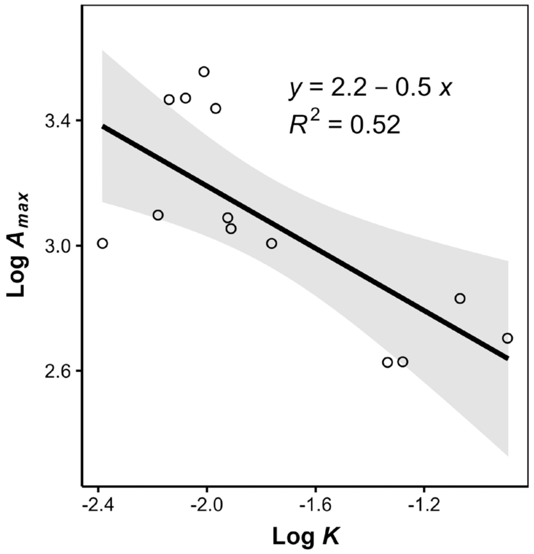

FIGURE 5 | Maximum estimated age ($A_{\max}$) decreases with von Bertalanffy growth model rate constant (K) across the study populations.

4 | Discussion

We provided key life history data by modelling the growth rates and longevity of 13 North American freshwater mussel populations, including two species with previously unquantified growth parameters. Below, we use this new life history information to hypothesise which life history strategy best characterises the study species, and what types of disturbance regimes they are best adapted to. Mussel growth was negatively related to longevity, but not to hydrologic summary statistics, suggesting that eco-evolutionary trade-offs have a stronger influence on mussel growth than environmental factors in the populations we studied.

4.1 | Growth Rates and Longevity

The estimates of growth rate and longevity that we presented here corresponded closely to the ranges of those reported for other populations and closely related taxa (Hopper et al. 2023). For example, species within the phylogenetic tribe Lampsilini are most often opportunistic or periodic strategists with relatively high growth rates and correspondingly short life spans (Haag 2012). In this study, we described growth trajectories for two lampsilines (*L. ovata* and *C. taeniatus*) that have not had their life history classification described. Yet the values of K and $A_{\max}$ that we report for both species align closely with those reported for periodic strategists including congeneric species such as *Lampsilis ornata* (K=0.382, $A_{\max}$=18 years) and

TABLE 3 | Spearman's correlation coefficients (p values in parentheses) for the relationships between standardised growth index and annual stream flow statistics.

River	Species	Annual mean discharge	Annual median discharge	Annual CV of discharge	Annual high discharge days	Annual low discharge days	Growing season mean discharge	Growing season median discharge	Growing season CV of discharge	Growing season high discharge days	Growing season low discharge days
Bear Creek	*Amblema plicata*	0.40 (0.750)	0.20 (0.917)	−1.00 (0.0833)	−1.00 (0.083)	−0.20 (0.917)	1.00 (0.083)	1.00 (0.083)	0.20 (0.917)	−0.80 (0.333)	1.00 (0.083)
	Cyclonaias tuberculata	0.80 (0.333)	0.40 (0.750)	−0.80 (0.333)	−0.80 (0.333)	0.40 (0.750)	0.80 (0.333)	0.80 (0.333)	0.40 (0.75)	−0.40 (0.750)	0.80 (0.333)
	Lampsilis ovata	0.40 (0.750)	0.80 (0.333)	−0.40 (0.75)	−0.40 (0.750)	0.00 (1.000)	0.40 (0.750)	0.40 (0.750)	0.80 (0.333)	−0.80 (0.333)	0.40 (0.750)
	Pustulosa pustulosa	−0.60 (0.417)	−0.80 (0.333)	−0.40 (0.75)	−0.40 (0.750)	−0.80 (0.333)	0.40 (0.750)	0.40 (0.750)	−0.80 (0.333)	−0.20 (0.917)	0.40 (0.750)
Cahaba River	*Amblema plicata*	−0.15 (0.616)	0.05 (0.868)	−0.41 (0.15)	−0.01 (0.970)	−0.23 (0.435)	0.35 (0.221)	0.19 (0.522)	0.31 (0.273)	0.03 (0.927)	0.37 (0.196)
Duck River	*Amblema plicata*	−0.22 (0.332)	−0.04 (0.860)	0.099 (0.67)	−0.01 (0.969)	−0.19 (0.416)	−0.14 (0.550)	−0.07 (0.745)	−0.27 (0.242)	0.05 (0.843)	−0.22 (0.331)
	Cyclonaias tuberculata	0.09 (0.698)	0.26 (0.243)	−0.033 (0.884)	−0.30 (0.171)	0.07 (0.764)	**0.52 (0.015)**	0.31 (0.160)	0.42 (0.0545)	−0.18 (0.410)	0.36 (0.098)
	Pustulosa pustulosa	−0.12 (0.529)	−0.25 (0.191)	**0.41 (0.033)**	0.14 (0.478)	−0.19 (0.346)	−0.09 (0.649)	−0.18 (0.353)	−0.16 (0.405)	0.22 (0.254)	−0.15 (0.455)
	Cambarunio taeniatus	0.02 (0.952)	−0.06 (0.844)	0.49 (0.0809)	0.20 (0.502)	0.13 (0.671)	−0.01 (0.964)	−0.21 (0.464)	0.055 (0.856)	0.25 (0.391)	−0.23 (0.426)
Paint Rock	*Amblema plicata*	−0.32 (0.173)	−0.20 (0.396)	−0.29 (0.207)	0.20 (0.400)	−0.17 (0.482)	−0.38 (0.103)	−0.24 (0.309)	**−0.72 (< 0.001)**	0.31 (0.184)	−0.31 (0.187)
	Cyclonaias tuberculata	−0.35 (0.104)	−0.38 (0.070)	**0.48 (0.023)**	0.37 (0.083)	−0.38 (0.072)	−0.34 (0.111)	−0.35 (0.102)	−0.27 (0.211)	0.36 (0.096)	−0.31 (0.154)
	Lampsilis ovata	**−0.59 (0.014)**	−0.45 (0.073)	−0.083 (0.751)	**0.63 (0.007)**	−0.47 (0.056)	−0.39 (0.118)	−0.42 (0.095)	−0.46 (0.0645)	**0.65 (0.005)**	−0.39 (0.118)
	Pustulosa pustulosa	−0.09 (0.687)	0.22 (0.320)	−0.1 (0.643)	−0.21 (0.353)	−0.09 (0.702)	0.15 (0.498)	0.15 (0.511)	−0.24 (0.285)	−0.18 (0.422)	0.13 (0.566)
Mean correlation		−0.06	−0.02	−0.16	−0.12	−0.16	0.17	0.14	−0.06	−0.05	0.14

Note: Bolded values indicate $p < 0.05$. The bottom row shows the mean correlation coefficient for each stream flow statistic across all populations.

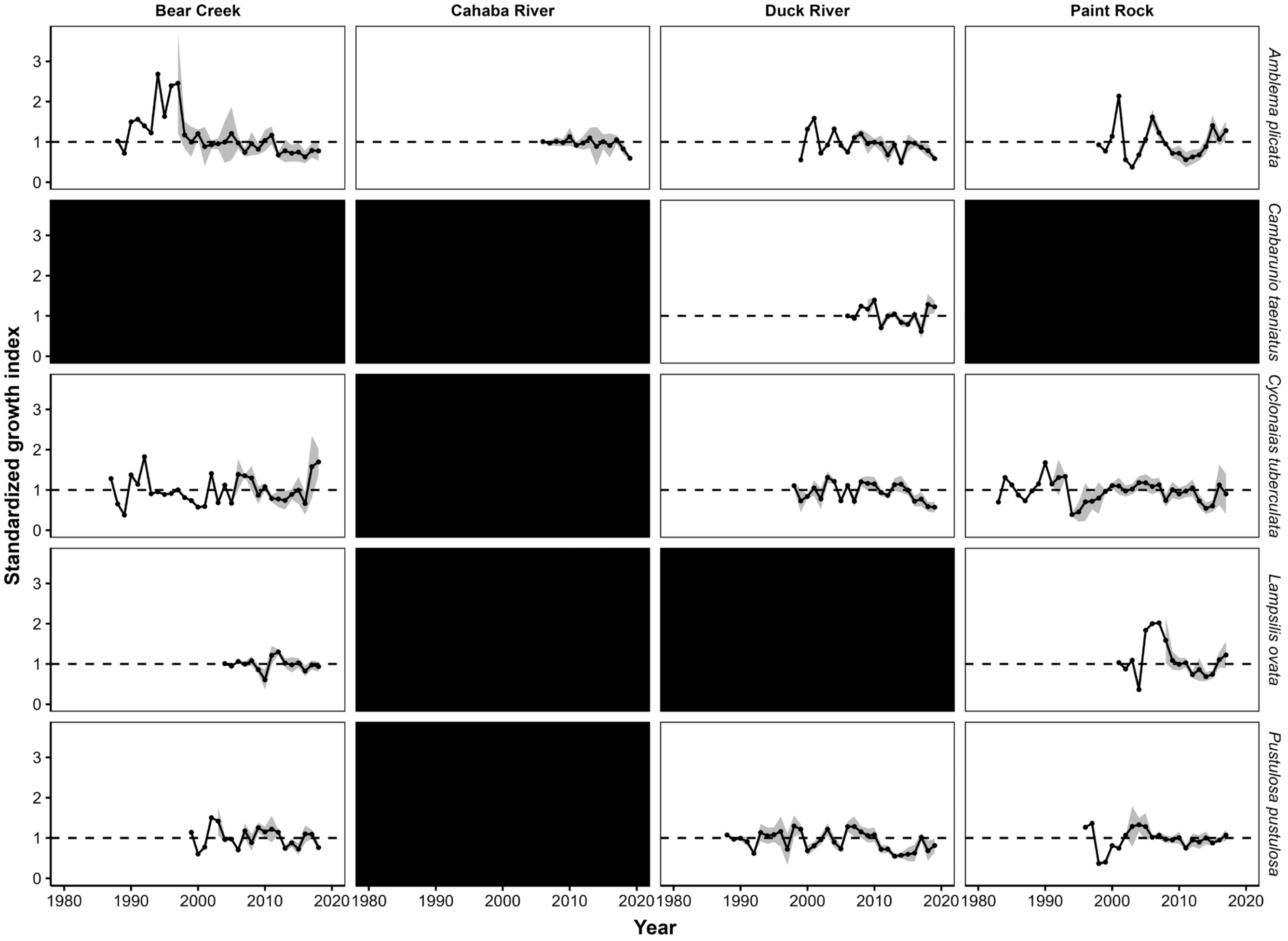

FIGURE 6 | Standardised master growth chronologies for each study population. Filled black boxes represent species that were not sampled at a site, due to their absence or low abundance. Points show population mean standardised growth indices. Grey ribbons show ±1 standard error around the mean for time points where $n > 1$.

Cambarunio nebulosus ($K = 0.232$–0.477, $A_{\max} = 12$ years) (Haag and Rypel 2011). We hypothesise that *L. ovata* and *C. taeniatus* may also be best classified as periodic or opportunistic strategists. These species are likely best adapted to small- to medium-sized rivers that have unpredictable or extreme disturbance regimes (Haag 2012; Hornbach, Sietman, and William 2024).

Similarly, our estimates of K and $A_{\max}$ for *C. tuberculata* (tribe Quadrulini) fell within the range of previous studies which characterise this species as slow-growing and long-lived ($K = 0.094$–0.164, $A_{\max} = 36$–91 years) (Jirka 1986). Most quadriline mussels are equilibrium strategists, so we hypothesise that *C. tuberculata* is likely also best classified as an equilibrium species based on their growth rates, fitting with the findings of previous studies (Haag 2012; Moore et al. 2021). Previously reported growth parameters for *P. pustulosa* (tribe Quadrulini, $K = 0.051$–0.143, $A_{\max} = 25$–48) and *A. plicata* (tribe Amblemini, $K = 0.074$–0.207, $A_{\max} = 13$–79) vary substantially among populations (Christian et al. 2000; Haag and Rypel 2011; Sansom, Atkinson, and Vaughn 2016; DuBose et al. 2022). Our estimates of K and $A_{\max}$ for *P. pustulosa* and *A. plicata* also varied broadly among populations. Although variable, our estimates support existing classifications of *P. pustulosa* as an equilibrium strategist (Haag 2012; Moore et al. 2021). *Amblema plicata* is also considered to be an equilibrium strategist; however, Haag (2012) identified a "short-lived" population of *A. plicata* that more closely resembled a periodic strategist. Similarly, our estimates of K and $A_{\max}$ for *A. plicata* span values that are characteristic of both equilibrium and periodic strategists. Most likely, *C. tuberculata* and *P. pustulosa* are best adapted to stable habitats characteristic of mid-sized and large rivers, while *A. plicata* is probably a stream-size generalist given its seemingly plastic life history (Haag 2012; Hornbach, Sietman, and William 2024).

Our expectation that longevity ($A_{\max}$) would be related to growth rate (K) across populations was also supported, and matches relationships identified for other mussel species (Haag and Rypel 2011). This pattern supports the fundamental eco-evolutionary prediction that longevity decreases as growth rate increases (Metcalfe 2003). The ecological implications of this trade-off between growth and longevity are demonstrated by the life history strategy classifications that we hypothesised for our focal species. The lampsiline species *L. ovata* and *C. taeniatus* have traits that characterise periodic strategists. Thus, they should reach maturity and reproduce faster as well and may be more competitive in cyclically disturbed environments where the time to reach maturity is shorter than the disturbance interval. The quadriline species *C. tuberculata* and *P. pustulosa* have traits that characterise equilibrium strategists, and these species should require a longer time to reach maturity. As such, *C. tuberculata* and *P. pustulosa* should be most competitive in stable environments that allow sufficient intervals for these species to reach maturity in between major disturbance events. *Amblema plicata*, on the other hand, seems to be more phenotypically plastic in its life history traits than other mussel species. This plasticity may be due to genetic differences or perhaps this species is simply more responsive to environmental perturbations that alter growth and longevity. For example, we anticipated that variation in temperature among streams might lead to variation in growth rates among populations. However, the study rivers with the fastest-growing populations were not necessarily those with the greatest number of growing degree days or the longest growing seasons. Regardless of the underlying mechanisms, the plastic life history of *A. plicata* may enable this species to be competitive across a range of disturbance regimes. This suggestion is supported by the fact that *A. plicata* inhabits a broad range of ecoregions and habitats in North America (Haag 2012; Graf and Cummings 2021).

4.2 | Stream Flow and Annual Growth

Contrary to our expectations, we found little evidence that annual growth was related to stream flow in our study. Other studies have suggested that mussel growth is strongly influenced by factors associated with discharge (Rypel, Haag, and Findlay 2008, 2009; Black et al. 2010, 2015; Haag and Rypel 2011). It is possible that we made more interpretive errors than these other studies, as the annuli in mussel shell sections are notoriously difficult to identify without validation through mark-recapture studies, although cross-dating is considered a viable alternative (Rypel, Haag, and Findlay 2008). Further, growth chronologies that are short in duration and the presence of impoundments or other human-generated disturbances can obscure the relationship between annual growth and streamflow (Rypel, Haag, and Findlay 2008, 2009; Sansom et al. 2013). Of the present study rivers, Bear Creek and the Duck River are impounded; further, Bear Creek had a relatively short period of record for its stream gage (2015–2018) and the biochronology for the Cahaba River could only be dated back 14 years (2006–2019). The ecological integrity of the Cahaba River is also threatened by the urbanisation of the surrounding catchment, which includes the metropolitan centre of Birmingham, AL.

It is also possible that discharge is simply not a universal predictor of mussel growth. Even studies that have validated annuli over multiple years have only reported correlations that were statistically significant in 57% of cases ($n = 37$, $\alpha = 0.05$) (Haag and Rypel 2011). The strength and direction of correlations between mussel growth and stream flow also vary among populations of the same species living under different environmental contexts (Rypel, Haag, and Findlay 2009; Black et al. 2010). More complex hydrodynamic factors such as shear stress and Reynolds number are more closely related to the presence, abundance, and species composition of mussel communities at local scales than hydrologic variables like discharge (Lopez and Vaughn 2021). The same may be true of mussel growth, but that hypothesis remains untested.

Annual growth in our study system may be limited by factors other than flow. For example, annual temperature changes might mask flow-related changes in growth. Our temperature data were limited to the duration of a recent data logger deployment, so we could only generally characterise the recent temperature regimes of the study rivers. However, prior tests of this hypotheses suggest that correlations between flow and annual growth are more consistent and often stronger than those between temperature and annual growth—although temperature is key at sub-annual scales (Rypel, Haag, and Findlay 2008; Black et al. 2010; Brewer, Grossman, and Randklev 2024). Alternatively, mussel growth might be food-limited in our study systems, but the existing understanding of mussel food web ecology remains too limited to empirically assess this hypothesis (Aldridge et al. 2022). Ultimately, the strength of relationships between mussel growth and environmental variables inherently depends on local conditions, phylogenetic constraints, and the scale of observation.

5 | Conclusions

Our findings highlight the need for species- and population-specific conservation efforts for freshwater mussels. While some species seem to have relatively narrow ranges for growth and longevity, the growth of other species can vary widely among populations to the point that some species can seemingly exhibit different life history strategies depending on location. A comprehensive understanding of growth and longevity parameters is therefore key to predicting how freshwater species may respond to changing climatic and flow regimes or other ecological factors such as resource availability and habitat characteristics. For mussels, information on life history traits should in turn be integrated with knowledge about other species traits including thermal tolerance guilds, host preferences for mussels' parasitic larvae, and movement behaviour (Spooner et al. 2011; Gough, Gascho Landis, and Stoeckel 2012; Gates, Vaughn, and Julian 2015; Lopez et al. 2022). Given the important ecosystem services that mussels and related freshwater species provide (Atkinson et al. 2023), along with their widespread distributions and high rates of imperilment (Böhm et al. 2021; Graf and Cummings 2021), a more thorough understanding of mussel life history traits—and how those traits mediate their relationships with other freshwater taxa and the environment—is imperative.

Author Contributions

Conceptualisation: G.W.H., J.W.L., I.A.B., C.L.A. Developing methods: G.W.H., I.A.B., J.W.L. Conducting the research: I.A.B., J.W.L., G.W.H., I.S.G., C.L.A. Data analysis: I.A.B., J.W.L. Data interpretation: I.A.B., J.W.L. Preparation of figures and tables: I.A.B., J.W.L., I.S.G. Writing: I.A.B., J.W.L., G.W.H., I.S.G., C.L.A.

Acknowledgements

This study was funded by NSF DEB-1831512 to CLA. Native mussels were collected under USFWS permit #TE68616B-1 and ALCDNR permit #2020097718468680 and permit #2016077745468680 issued to CLA. We thank F Andrus for assistance with shell sectioning. We also thank the many individuals who assisted with field sampling during mussel surveys, and two anonymous reviewers for helpful comments that improved the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in this study are publicly available at https://doi.org/10.6084/m9.figshare.26371267.v1.

[Correction added on 18 January 2025, after first online publication: Data Availability is updated in this version.]

References

Aldridge, D. C. 1999. "The Morphology, Growth and Reproduction of Unionidae (Bivalvia) in a Fenland Waterway." *Journal of Molluscan Studies* 65: 47–60. https://doi.org/10.1093/mollus/65.1.47.

Aldridge, D. C., I. S. Ollard, Y. V. Bespalaya, et al. 2022. "Freshwater Mussel Conservation: A Global Horizon Scan of Emerging Threats and Opportunities." *Global Change Biology* 29: 575–589.

Atkinson, C. L., G. W. Hopper, D. A. Kreeger, et al. 2023. "Gains and Gaps in Knowledge Surrounding Freshwater Mollusk Ecosystem Services." *Freshwater Mollusk Biology and Conservation* 26: 20–31.

Black, B. A., G. W. Boehlert, and M. M. Yoklavich. 2005. "Using Tree-Ring Crossdating Techniques to Validate Annual Growth Increments in Long-Lived Fishes." *Canadian Journal of Fisheries and Aquatic Sciences* 62: 2277–2284. https://doi.org/10.1139/f05-142.

Black, B. A., J. B. Dunham, B. W. Blundon, J. Brim-Box, and A. J. Tepley. 2015. "Long-Term Growth-Increment Chronologies Reveal Diverse Influences of Climate Forcing on Freshwater and Forest Biota in the Pacific Northwest." *Global Change Biology* 21: 594–604. https://doi.org/10.1111/gcb.12756.

Black, B. A., J. B. Dunham, B. W. Blundon, M. F. Raggon, and D. Zima. 2010. "Spatial Variability in Growth-Increment Chronologies of Long-Lived Freshwater Mussels: Implications for Climate Impacts and Reconstructions." *Écoscience* 17: 240–250. https://doi.org/10.2980/17-3-3353.

Bleasdale, A., A. Browne, D. Byrne, et al. 2020. "The KerryLIFE Freshwater Pearl Mussel Conservation Project." In *Farming for Nature: The Role of Results-Based Payments*, edited by E. O'Rourke and J. A. Finn, 148–183. Wexford, Ireland: Teagasc and National Parks and Wildlife Service.

Blevins, E., L. McMullen, S. Jepsen, M. Blackburn, A. Code, and S. H. Black. 2019. *Mussel-Friendly Restoration: A Guide to the Essential Steps for Protecting Freshwater Mussels in Aquatic and Riparian Restoration, Construction, and Land Management Projects and Activities*. Portland, OR, USA: Xerces Society for Invertebrate Conservation.

Böhm, M., N. I. Dewhurst-Richman, M. Seddon, et al. 2021. "The Conservation Status of the world's Freshwater Molluscs." *Hydrobiologia* 848: 3231–3254. https://doi.org/10.1007/s10750-020-04385-w.

Brewer, M. A., E. L. Grossman, and C. R. Randklev. 2024. "Clumped Isotopes Reveal Relationship Between Mussel Growth and River Discharge." *Scientific Reports* 14: 7653.

Bucholz, J. R., G. W. Hopper, I. S. González, et al. 2023. "Community-Wide Correlations Between Species Richness, Abundance and Population Genomic Diversity in a Freshwater Biodiversity Hotspot." *Molecular Ecology* 32: 5894–5912. https://doi.org/10.1111/mec.16991.

Bunn, A., M. Korpela, F. Biondi, et al. 2023. "dplR: Dendrochronology Program Library in R."

Bunn, A. G. 2008. "A Dendrochronology Program Library in R (dplR)." *Dendrochronologia* 26: 115–124. https://doi.org/10.1016/j.dendro.2008.01.002.

Bunn, A. G. 2010. "Statistical and Visual Crossdating in R Using the dplR Library." *Dendrochronologia* 28: 251–258. https://doi.org/10.1016/j.dendro.2009.12.001.

Christian, A. D., C. L. Davidson, W. R. P. Ii, et al. 2000. "Growth Curves of Four Species of Commercially Valuable Freshwater Mussels (Bivalva: Unionidae)." *Journal of the Arkansas Academy of Science* 54: 9.

Cook, E. R., and K. Peters. 1981. "The Smoothing Spline: A New Approach to Standardizing Forest Interior Tree-Ring Width Series for Dendroclimatic Studies." *Tree-Ring Bulletin* 41: 45–53.

DuBose, T. P., M. A. Patten, A. S. Holt, and C. C. Vaughn. 2022. "Latitudinal Variation in Freshwater Mussel Potential Maximum Length in Eastern North America." *Freshwater Biology* 67: 1020–1034. https://doi.org/10.1111/fwb.13898.

Elkins, D., S. C. Sweat, B. R. Kuhajda, A. L. George, K. S. Hill, and S. J. Wenger. 2019. "Illuminating Hotspots of Imperiled Aquatic Biodiversity in the Southeastern US." *Global Ecology and Conservation* 19: e00654. https://doi.org/10.1016/j.gecco.2019.e00654.

Freshwater Mollusk Conservation Society. 2016. "A National Strategy for the Conservation of Native Freshwater Mussels." *Freshwater Mollusk Biology and Conservation* 19: 1–21. https://doi.org/10.31931/fmbc.v19i1.2016.1-21.

Freshwater Mollusk Conservation Society. 2023. "The 2023 FMCS checklist of freshwater mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada."

Fritts, H. C. 1976. *Tree Rings and Climate*. London, UK: Academic Press.

Gagnon, P. M., S. W. Golladay, W. K. Michener, and M. C. Freeman. 2004. "Drought Responses of Freshwater Mussels (Unionidae) in Coastal Plain Tributaries of the Flint River Basin, Georgia." *Journal of Freshwater Ecology* 19: 667–679. https://doi.org/10.1080/02705060.2004.9664749.

Gates, K. K., C. C. Vaughn, and J. P. Julian. 2015. "Developing Environmental Flow Recommendations for Freshwater Mussels Using the Biological Traits of Species Guilds." *Freshwater Biology* 60: 620–635. https://doi.org/10.1111/fwb.12528.

Gough, H. M., A. M. Gascho Landis, and J. A. Stoeckel. 2012. "Behaviour and Physiology Are Linked in the Responses of Freshwater Mussels to Drought: Differential Mussel Responses to Drought." *Freshwater Biology* 57: 2356–2366. https://doi.org/10.1111/fwb.12015.

Graf, D. L., and K. S. Cummings. 2021. "A 'Big Data' Approach to Global Freshwater Mussel Diversity (Bivalvia: Unionoida), with an Updated Checklist of Genera and Species." *Journal of Molluscan Studies* 87: eyaa034. https://doi.org/10.1093/mollus/eyaa034.

Grissino-Mayer, H. 2001. "Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA." *TreeRing Research* 57: 205–221.

Haag, W. R. 2012. *North American Freshwater Mussels: Natural History, Ecology, and Conservation*. New York, NY, USA: Cambridge University Press.

Haag, W. R., A. K. Burrow, T. P. DuBose, and S. J. Price. 2024. "A Broadly Applicable, Objective Freshwater Mussel Assemblage Health Index (MAHI)." *Freshwater Science* 43: 150–168. https://doi.org/10.1086/730378.

Haag, W. R., and A. M. Commens-Carson. 2008. "Testing the Assumption of Annual Shell Ring Deposition in Freshwater Mussels." *Canadian Journal of Fisheries and Aquatic Sciences* 65: 493–508. https://doi.org/10.1139/f07-182.

Haag, W. R., J. J. Culp, M. A. McGregor, R. Bringolf, and J. A. Stoeckel. 2019. "Growth and Survival of Juvenile Freshwater Mussels in Streams: Implications for Understanding Enigmatic Mussel Declines." *Freshwater Science* 38: 770. https://doi.org/10.1086/705919.

Haag, W. R., and A. L. Rypel. 2011. "Growth and Longevity in Freshwater Mussels: Evolutionary and Conservation Implications." *Biological Reviews* 86: 225–247. https://doi.org/10.1111/j.1469-185X.2010.00146.x.

Haney, A., H. Abdelrahman, and J. A. Stoeckel. 2020. "Effects of Thermal and Hypoxic Stress on Respiratory Patterns of Three Unionid Species: Implications for Management and Conservation." *Hydrobiologia* 847: 787–802. https://doi.org/10.1007/s10750-019-04138-4.

Holmes, R. L. 1983. "Computer-Assisted Quality Control in Tree-Ring Dating and Measurement." *Tree-Ring Bulletin* 43: 51–67.

Hopper, G. W., J. R. Bucholz, T. P. DuBose, et al. 2023. "A Trait Dataset for Freshwater Mussels of The United States of America." *Scientific Data* 10: 745. https://doi.org/10.1038/s41597-023-02635-9.

Hopper, G. W., S. Chen, G. I. Sánchez, J. R. Bucholz, Y. Lu, and C. L. Atkinson. 2021. "Aggregated Filter-Feeders Govern the Flux and Stoichiometry of Locally Available Energy and Nutrients in Rivers." *Functional Ecology* 35: 1183–1195. https://doi.org/10.1111/1365-2435.13778.

Hornbach, D. J., B. E. Sietman, and B. R. William. 2024. "The Relationship Between Stream Size and Life-History Traits in Freshwater Mussels: An Examination of the Host-Habitat Continuum Concept." *Hydrobiologia* 851: 4419–4437. https://doi.org/10.1007/s10750-024-05595-2.

Hornbach, D. J., H. N. Stutzman, M. C. Hove, et al. 2021. "Influence of Surrounding Land-Use on Mussel Growth and Glycogen Levels in the St. Croix and Minnesota River Basins." *Hydrobiologia* 848: 3045–3063. https://doi.org/10.1007/s10750-019-04016-z.

IPCC. 2023. "Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change." Geneva, Switzerland.

Jirka, K. J. 1986. "Reproductive biology and growth rates of selected species of freshwater mussels (Bivalvia: Unionidae) in the New and Greenbrier rivers, Virginia and West Virginia." Virginia Polytechnic Institute and State University, Blacksburg, VA, USA.

Lea, E. 1910. "Contributions to the Methodics in Herring-Investigations." *ICES Journal of Marine Science* s1: 7–33. https://doi.org/10.1093/icesjms/s1.53.7.

Lopes-Lima, M., L. E. Burlakova, A. Y. Karatayev, K. Mehler, M. Seddon, and R. Sousa. 2018. "Conservation of Freshwater Bivalves at the Global Scale: Diversity, Threats and Research Needs." *Hydrobiologia* 810: 1–14. https://doi.org/10.1007/s10750-017-3486-7.

Lopez, J. W., T. P. DuBose, A. J. Franzen, C. L. Atkinson, and C. C. Vaughn. 2022. "Long-Term Monitoring Shows That Drought Sensitivity and Riparian Land Use Change Coincide With Freshwater Mussel Declines." *Aquatic Conservation: Marine and Freshwater Ecosystems* 32: 1571–1583. https://doi.org/10.1002/aqc.3884.

Lopez, J. W., and C. C. Vaughn. 2021. "A Review and Evaluation of the Effects of Hydrodynamic Variables on Freshwater Mussel Communities." *Freshwater Biology* 66: 1665–1679. https://doi.org/10.1111/fwb.13784.

Metcalfe, N. 2003. "Growth Versus Lifespan: Perspectives From Evolutionary Ecology." *Experimental Gerontology* 38: 935–940. https://doi.org/10.1016/S0531-5565(03)00159-1.

Moore, A. P., N. Galic, R. A. Brain, D. J. Hornbach, and V. E. Forbes. 2021. "Validation of Freshwater Mussel Life-History Strategies: A Database and Multivariate Analysis of Freshwater Mussel Life-History Traits." *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 3386–3402. https://doi.org/10.1002/aqc.3713.

Neemuchwala, S., N. A. Johnson, J. M. Pfeiffer, et al. 2023. "Coevolution With Host Fishes Shapes Parasitic Life Histories in a Group of Freshwater Mussels (Unionidae: Quadrulini)." *Bulletin of the Society of Systematic Biology* 2: 1–25. https://doi.org/10.18061/bssb.v2i1.

Ogle, D. H. 2022. "RFishBC: Back-Calculation of Fish Length."

Reid, A. J., A. K. Carlson, I. F. Creed, et al. 2019. "Emerging Threats and Persistent Conservation Challenges for Freshwater Biodiversity." *Biological Reviews* 94: 849–873. https://doi.org/10.1111/brv.12480.

Rypel, A. L., W. R. Haag, and R. H. Findlay. 2008. "Validation of Annual Growth Rings in Freshwater Mussel Shells Using Cross Dating." *Canadian Journal of Fisheries and Aquatic Sciences* 65: 2224–2232. https://doi.org/10.1139/F08-129.

Rypel, A. L., W. R. Haag, and R. H. Findlay. 2009. "Pervasive Hydrologic Effects on Freshwater Mussels and Riparian Trees in Southeastern Floodplain Ecosystems." *Wetlands* 29: 497–504. https://doi.org/10.1672/08-109.1.

Sæther, B.-E., T. H. Ringsby, E. Røskaft, B.-E. Saether, and E. Roskaft. 1996. "Life History Variation, Population Processes and Priorities in Species Conservation: Towards a Reunion of Research Paradigms." *Oikos* 77: 217. https://doi.org/10.2307/3546060.

Sansom, B. J., C. L. Atkinson, and C. C. Vaughn. 2016. "Growth and Longevity Estimates for Mussel Populations in Three Ouachita Mountain Rivers." *Freshwater Mollusk Biology and Conservation* 19: 19. https://doi.org/10.31931/fmbc.v19i2.2016.19-26.

Sansom, B. J., D. J. Hornbach, M. C. Hove, and J. S. Kilgore. 2013. "Effects of Flow Restoration on Mussel Growth in a Wild and Scenic North American River." *Aquatic Biosystems* 9: 6. https://doi.org/10.1186/2046-9063-9-6.

Spooner, D. E., M. A. Xenopoulos, C. Schneider, and D. A. Woolnough. 2011. "Coextirpation of Host-Affiliate Relationships in Rivers: The Role of Climate Change, Water Withdrawal, and Host-Specificity." *Global Change Biology* 17: 1720–1732. https://doi.org/10.1111/j.1365-2486.2010.02372.x.

Strayer, D. L., J. A. Downing, W. R. Haag, et al. 2004. "Changing Perspectives on Pearly Mussels, North America's Most Imperiled Animals." *Bioscience* 54: 429. https://doi.org/10.1641/0006-3568(2004)054[0429:cpopmn]2.0.co;2.

Strayer, D. L., and D. Dudgeon. 2010. "Freshwater Biodiversity Conservation: Recent Progress and Future Challenges." *Journal of the North American Benthological Society* 29: 344–358. https://doi.org/10.1899/08-171.1.

Winemiller, K. O., and K. A. Rose. 1992. "Patterns of Life-History Diversification in North American Fishes: Implications for Population Regulation." *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2196–2218. https://doi.org/10.1139/f92-242.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.