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REGULAR ARTICLE

AGE, ASYMPTOTIC SIZE, AND GROWTH CONSTANTS OF EAST TEXAS FRESHWATER UNIONID MUSSELS

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ABSTRACT

Age and growth information helps researchers better understand how freshwater mussels (Bivalvia: Unionida)—among the most imperiled aquatic fauna worldwide—cope with environmental change. Shell thin sectioning is the primary method for estimating age and growth. Using a low-speed saw, a thin, radial cross-section of shell is taken and then mounted on an unfrosted microscope slide and read using a dissecting microscope. Thin sectioning can be time intensive, and species-specific issues, such as crowded annuli, can complicate efforts to provide accurate estimates. To date, only 69 of the approximately 300 North American species have age and growth information. Texas illustrates this issue perfectly; population-specific growth estimates are available for only 6 of the 52 species known to occur in the state. For the remaining species, information is either unavailable or inferred from closely related congeners or populations outside the state. This is problematic because incorrect inferences about age and growth can lead to erroneous assumptions about a species' life history, which could result in management and conservation actions that, at best, waste resources, and at worst, lead to population declines. We thin-sectioned eight different mussel species, including three species of conservation concern, then estimated growth parameters using von Bertalanffy growth curves. Our work more than doubled the number of Texas species with age and growth information from populations within the state. We found that growth serves as a good proxy for species position along a continuum contrasting higher growth and shorter lifespans versus lower growth and longer lifespans. Our results should be useful for making inferences about how species respond to environmental change.

KEY WORDS: Age, growth, Texas, freshwater mussel, von Bertalanffy, life history, unionid

INTRODUCTION

Freshwater mussels (Bivalvia: Unionida) are among the most imperiled aquatic fauna worldwide (Lydeard et al. 2004; Strayer et al. 2004; Lopes-Lima et al. 2018; Ferreira-Rodríguez et al. 2019; Böhm et al. 2021). In the USA, where they reach their greatest diversity, an estimated 65% of the approximately 300 described species have some conservation designation (Williams et al. 1993, 2008; Lydeard et al. 2004; Strayer et al. 2004; Haag and Williams 2014). Efforts to mitigate the decline of freshwater mussels are complicated by significant information gaps, such as species life-history strategies (Haag 2012). Life-history strategies provide a framework for classifying and comparing species on the basis of features that represent an optimization of trade-offs between growth, survival, and reproduction to maximize fitness to specific environments (MacArthur and Wilson 1967; Pianka 1970; Stearns 1992; Winemiller 2005; Kozlowski 2006; Albaladejo-Robles et al. 2023). Of these, growth has been shown to be an indicator of the position or "speed" of a species along the *r/K* continuum (Haag and Rypel 2011), which

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contrasts species on the basis of their investment in offspring and different population-regulation mechanisms (MacArthur and Wilson 1967; Pianka 1970; Stearns 1992; Winemiller 2005; Kozlowski 2006; Albaladejo-Robles et al. 2023).

According to *r*/*K* selection theory, fast-growing or *r*-selected species are adapted to density-independent influences, such as disturbance events, and they possess a suite of attributes (i.e., short lifespans, small bodies, and high fecundity) that allows them to recover quickly (MacArthur and Wilson 1967; Pianka 1970; Stearns 1992; Haag 2012; Albaladejo-Robles et al. 2023). In contrast, slow-growing or *K*-selected species are adapted to density-dependent influences, such as competition and predation, and are unable to recover quickly from disturbance events (MacArthur and Wilson 1967; Pianka 1970; Stearns 1992; Winemiller 2005; Haag 2012; Albaladejo-Robles et al. 2023). For this reason, slow-growing species are usually considered more sensitive to environmental changes, whereas fast-growing species are considered more tolerant (Albaladejo-Robles et al. 2023). *r*/*K* selection theory is the basis for more complex life-history models (e.g., competitive–stress tolerant–ruderal [C-S-R] or equilibrium–periodic–opportunistic [E-P-O]; Grime 1977, 1979; Southwood 1977; Winemiller and Rose 1992; Haag 2012), but these models require additional life-history information, which is often unavailable for rare or understudied species. In Texas, life-history data for many species remain incomplete, presenting challenges in applying more complex life-history models. Critical parameters, such as age at maturity and reproductive effort, are frequently unknown for numerous taxa, limiting the ability to accurately categorize species within frameworks like the C-S-R or the E-P-O models. Thus, *r*/*K* selection theory provides a straightforward and useful framework for evaluating how species may cope with environmental change and for assessing extinction risk and sensitivity to management and conservation actions at the population level, especially when only age and growth are known (Hastie et al. 2000; Haag 2012; Albaladejo-Robles et al. 2023).

Freshwater mussels deposit annual growth rings, hereafter annuli, in their shells, which can be used to estimate age, growth, and longevity (Neves and Moyer 1988; Haag and Commens-Carson 2008). Thin sectioning is the primary method for identifying annuli. Using a low-speed saw, a thin, radial cross-section of shell is taken and then mounted on an unfrosted microscope slide. Independent observers then use a dissecting microscope to count the annuli to determine age and measure the distance between annuli to estimate annual growth (Neves and Moyer 1988; Haag and Commens-Carson 2008; Haag and Rypel 2011). This method can be time intensive and species-specific issues, such as crowded annuli, can complicate efforts to provide accurate estimates. To date, only 69 of approximately 300 North American species have age and growth information available, and much of what is known is drawn from a limited number of species from a narrow geographic area (Haag and Rypel 2011; Moore et al. 2021; Hopper et al. 2023). Texas is a perfect illustration of the lack of age and growth data. Currently, information is available for only 6 (*Amblema plicata*, *Fusconaia mitchelli*, *Lampsilis bracteata*, *Pleurobema riddellii*, *Pustulosa necki*, and *Pustulosa petrina*) of the 52 species known to occur in the state (Dudding et al. 2020; Ford et al. 2020; DuBose et al. 2022; de Moulpied et al. 2024). For the remaining species, age and growth information is either unavailable or is inferred from populations outside of the state or from closely related congeners (Randklev et al. 2023), neither of which may provide accurate data. Growth can vary across populations of the same species within the same river system (Sansom et al. 2016), between river systems (Haag and Rypel 2011), and latitudinally (DuBose et al. 2022). For example, Sansom et al. (2016) suggest that variations in discharge patterns may drive growth differences within river systems. Haag and Rypel (2011) highlight the role of water chemistry in influencing shell growth, whereas Dubose et al. (2022) found that water temperature plays a significant role in determining growth rates. These findings emphasize the need for population-specific data when applying life-history models, as broad generalizations on the basis of related species or geographically distant populations could lead to misclassifications.

We aimed to address the lack of life-history information for mussels by quantifying observable age, asymptotic size, and the Brody growth constant *K*. Our specific objectives were to (1) estimate age and *K* using thin sectioning for eight species, including several species of conservation concern; (2) compile age and growth information for other species in Texas using literature reports; and (3) describe patterns of longevity across phylogenetic groups and across and within species.

METHODS

Study Sites

We collected freshwater mussels at four sites across Texas in the Brazos River, the Sabine River, Village Creek, and the Lower Neches Valley Authority (LNVA) Canal within the Neches River basin (Fig. 1). The Brazos River is formed at the confluence of the Salt and Double Mountain forks in Stonewall County. The basin drains 117,870 km^2 and flows 1,509 km through Texas before entering the Gulf of Mexico (Brazos River Authority 2024). Near the collection site, the climate is subtropical humid (Texas Water Development Board 2012), with an air temperature range of 4.4–34.4°C and predominately agricultural land use (Griffith et al. 2007). The river near the collection site is slow flowing and generally silty with occasional visible bedrock.

The Sabine River drains a total area of 25,267 km^2 from its origin in Hunt County, Texas to the Gulf of Mexico (Texas Commision on Environmental Quality[TCEQ] 2002). The basin is heavily forested and is largely used for pasture, timber production, and livestock and poultry production (Griffith et al. 2007). The climate is predominately humid and

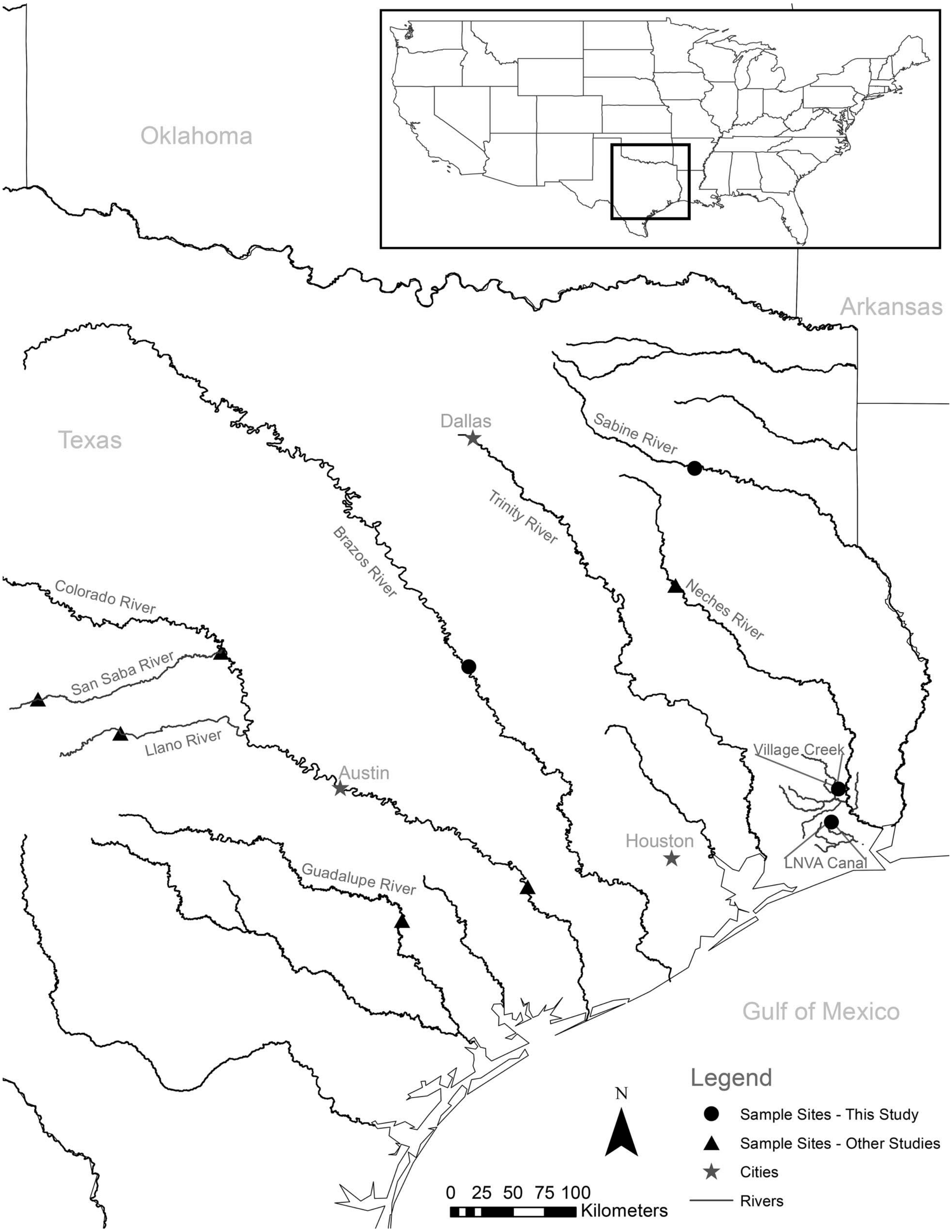

Figure 1. Collection sites for original data for this study and other studies where age and growth have been analyzed in Texas.

subtropical with an average annual rainfall of 1,016 mm (Sabine River Authority 2021) and an average annual air temperature range of 1.1–34.4°C near the collection site (Griffith et al. 2007). The river near the site can be flashy and the streambed is composed of cobble and gravel.

The Neches River originates near Colfax, Texas and flows for 669 km into Sabine Lake, an estuary of the Gulf of Mexico. Its watershed in southeast Texas drains 26,676 km^2 (Harrel and Hall 1991; Lower Neches Valley Authority 2024). We collected at two sites within the Neches River watershed, the LNVA canal and Village Creek; the climate for both is subtropical humid (Texas Water Development Board 2012). The LNVA Canal is in a predominately agricultural area and is used to supply water for local industry; it has a very fine silt substrate (Harrel and Hall 1991; Griffith et al. 2007). Rainfall in the area ranges from 939.8 to 1,447.8 mm annually, and air temperature ranges from 5.6 to 33.3°C. Village Creek is unregulated and is a major tributary of the lower Neches River (Khan et al. 2019). Mean annual rainfall for Village Creek is 193.8–1,473.2 mm and air temperature ranges from 4.4 to 33.3°C (Griffith et al. 2007). Near the sampling site, the river is generally slow flowing with a sandy substrate (Texas Parks and Wildlife Department [TPWD] 2016).

Study Species

The species analyzed in this study were *Pustulosa nodulata*, *Pustulosa pustulosa*, and *Quadrula quadrula* within the Quadrulini tribe, *Fusconaia askewi* and *Pleurobema. riddellii* within the Pleurobemini tribe, and *Lampsilis teres*, *Truncilla donaciformis*, and *Truncilla macrodon* within the Lampsilini tribe. Of these species, *F. askewi*, *Pl. riddellii*, and *T. macrodon* are considered state threatened (TPWD 2010, 2020); at the federal level, *Pl. riddellii* has been proposed for listing, and *T. macrodon* is currently listed, as threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 2023, 2024). At each site, we surveyed a search area not exceeding ∼150 m^2 both tactilely and visually for a total of 4 person-hours. We identified all live mussels to species and retained a subset of our focal species for thin sectioning. An effort was made to include a broad range of sizes to ensure a comprehensive representation of the age classes present in the population. We collected a total of 16 *Pl. riddellii*, 15 *Pu. nodulata*, 15 *Pu. pustulosa*, 10 *Q. quadrula*, and 15 *T. donaciformis* from the LNVA Canal and 16 *F. askewi* from Village Creek. We also collected 16 *Pu. pustulosa* and 10 *L. teres* from the Sabine River and 22 *T. macrodon* from the Brazos River in Central Texas.

Preparation and Interpretation of Shell Thin Sections

We prepared individuals for analysis by creating thin sections following Haag and Commens-Carson (2008). Specifically, shells were cleaned and dried, then one uncut valve was set in epoxy resin (craft resin creative liquid) on popsicle sticks. Once the resin was fully cured, we cut radial thin sections along the dorsal–ventral axis with a Buehler IsoMet 1000 precision cutter low-speed saw equipped with a diamond wafering blade (12.7 mm). Thin sections were mounted on glass microscope slides with Crystalbond 509 clear mounting adhesive (ThermoFisher Scientific) and sanded with progressively finer grits of wet-sanding blocks until annuli were clearly visible under light microscopy with an Olympus stereo microscope. We identified annuli for each thin section following Haag and Commens-Carson (2008). Specifically, a putative annulus must extend from the umbo through the periostracum without interruption and terminate through the prismatic layer. Juveniles were not available at our sample locations and so we back-calculated age and length for younger age classes. This was accomplished by aligning annuli that had been marked on the thin section with the raw edge of the corresponding cut valve to identify annuli on the outside of the shell. Once identified, these external annuli were then matched to the corresponding annuli on the uncut valve. Maximum length (i.e., the longest antero-posterior distance) of each external annulus on the uncut valve was then measured to estimate size at age for back-calculated ages. We also took the maximum length of the uncut valve and the observed age from the thin section and used this as the true length at age of the individual. Thus, we had a back-calculated length at age for each visible external annulus and a true length at age for when the individual was collected. We validated age estimates by using two independent readers. We reconciled any discrepancies by repeating the reading process until a consensus was reached or we removed the thin section from the data set. Outliers, that is, extreme ages relative to shell length, were identified by fitting growth curves (see below for details) with prediction intervals. Age estimates outside of the prediction intervals were reread and either included if the new estimate fell within the prediction interval or omitted if age–length discrepancies could not be reconciled. For the latter, if an unreconciled estimate was a back-calculated measurement, only that estimate was removed. If the unreconciled estimate was a true measurement, then the whole individual, including corresponding back-calculated estimates, was removed from the data set.

Growth and Longevity Estimates

To characterize growth and longevity for our focal species we fit the von Bertalanffy growth function (Ricker 1975) to length-at-age data

$$L_t = L_\infty(1 - e^{-K[t-t_0]}) \tag{1}$$

where L_t is the mean length at a given age (t in years); L_∞ is the asymptotic length, which represents the maximum mean length (mm) for a population; K is the Brody growth constant (yr^{-1}), which describes how quickly length approaches L_∞, and t_0 is the theoretical time in which $L = 0$ (Buckmeier et al. 2017). We also generated pseudo-R^2 values to gauge the fit of the data to the growth function. von Bertalanffy growth curves were fit to each population using the FSA (version 0.9.1; Ogle et al. 2022) and ntools (version 1.0.2; Baty et al.

Table 1. Population growth parameters for all species analyzed in this study derived from fitted von Bertalanffy growth curves. N = sample size; water body = sample collection site; pseudo-R^2 = coefficient of determination; L_∞ = predicted mean maximal length for the population; K = Brody growth constant; t_0 = theoretical time at which $L = 0$; and max age = maximum observed age. SE and 95% confidence intervals (CIs) are provided for each parameter estimate. LNVA = Lower Neches Valley Authority.

Species	Water Body	N	Pseudo-R^2	L_∞	L_∞ SE	CI Lower	CI Upper	K	K SE	CI Lower	CI Upper	t_0	t_0 SE	CI Lower	CI Upper	Max Age
Fusconaia askewi	Village Creek	9	0.96	56.81	1.50	54.36	59.95	0.19	0.02	0.14	0.24	−0.74	0.37	−1.64	−0.18	21
Lampsilis teres	Sabine River	9	0.97	139.78	2.82	134.68	145.74	0.34	0.03	0.28	0.39	0.39	0.13	0.12	0.62	13
Pleurobema riddellii	LNVA Canal	14	0.97	59.52	2.15	56.14	64.47	0.16	0.02	0.12	0.20	−1.26	0.32	−1.96	−0.74	18
Pustulosa nodulata	LNVA Canal	15	0.96	48.60	1.52	45.98	51.98	0.21	0.02	0.17	0.25	−0.43	0.16	−0.80	−0.15	15
Pustulosa pustulosa	Sabine River	15	0.95	65.91	2.40	61.72	71.22	0.13	0.02	0.10	0.16	−1.41	0.39	−2.31	−0.76	26
Pustulosa pustulosa	LNVA Canal	15	0.95	56.85	3.07	51.96	64.04	0.13	0.02	0.09	0.17	−1.42	0.41	−2.28	−0.75	20
Quadrula quadrula	LNVA Canal	10	0.96	53.02	2.10	49.66	58.20	0.16	0.02	0.12	0.21	−1.02	0.41	−1.94	−0.36	16
Truncilla donaciformis	LNVA Canal	10	0.95	41.19	2.16	38.17	46.72	0.25	0.04	0.17	0.33	−0.26	0.31	−0.96	0.18	10
Truncilla macrodon	Brazos River	22	0.96	57.82	3.63	52.73	66.84	0.20	0.03	0.14	0.26	−0.41	0.21	−0.91	−0.07	10

2015) packages in R (version 4.2.1; R Core Team 2022). To evaluate variation within populations of the same species, we compared growth parameters between the two populations of *Pu. pustulosa* for which we generated original data in this study. This was done by visually comparing confidence intervals (CIs) on K, L_∞, and t_0 values and concluding that nonoverlapping CIs are statistically significant.

Literature Review of Age and Growth

Using peer-reviewed literature reports, we compiled estimates of the von Bertalanffy growth parameters L_∞, K, and t_0 for species that occur within Texas (Hanson et al. 1988; Stoeckel et al. 1996; Morris and Corkum 1999; Christian et al. 2000; Anthony et al. 2001; Haag and Rypel 2011; Daniel and Brown 2014; Sansom et al. 2016; Dudding et al. 2020; Ford et al. 2020; DuBose et al. 2022; Hopper et al. 2023; de Moulpied et al. 2024). We included original data from this study plus reports for other species that are endemic to Texas or range within the state. For the latter, age and growth information is taken from populations that occur outside of Texas.

RESULTS

Age and Growth Variation among Species

We found K and L_∞ to vary across the eight species of Texas freshwater mussels we evaluated (Table 1). *Pustulosa pustulosa* from the Sabine River had the lowest growth constant with a K value of 0.13 (95% CI 0.10, 0.14) and *L. teres* from the Sabine River had the highest growth constant with a K value of 0.34 (95% CI 0.28, 0.39). Maximum observed age also varied with *Pu. pustulosa* from the Sabine River, being the longest-lived species at 26 yr and *T. macrodon* from the Brazos River being the shortest-lived species at 10 yr. Comparing growth parameters among major phylogenetic groups shows the Lampsilini tribe with the highest values for K (mean and range 0.26, 0.20–0.34 yr^{-1}) and both the largest (*L. teres*, 139.78 mm) and smallest (*T. donaciformis*, 41.19 mm) values for L_∞ in the study. The Quadrulini tribe had the lowest values for K (0.16, 0.13–0.21 yr^{-1}) and L_∞ ranged from 48.60 mm (*Pu. nodulata*) to 65.90 mm (*Pu. pustulosa*, Sabine River population). The Pleurobemini tribe, which included *Pl. riddellii* and *F. askewi*, had intermediate K values (0.17, 0.16–0.19 yr^{-1}) and L_∞ estimates of 59.52 mm and 56.81 mm, respectively.

Variation Among Populations

We compared two populations of *Pu. pustulosa* from the Sabine River in East Texas and the LNVA Canal in Southeast Texas. *Pustulosa pustulosa* from the Sabine River and the LNVA Canal had similar K values (i.e., 0.13), indicating slow growth for both subpopulations. However, L_∞ was higher for the subpopulation in the Sabine River (i.e., 65.91 mm) compared with the LNVA Canal subpopulations (i.e., 56.85 mm). The CIs for these estimates overlap (Table 1), which indicates the estimates are not significantly different. Maximum observed age for the Sabine River population was 26 yr, whereas the maximum observed age for the LNVA Canal population was 20 yr.

Literature Review of Growth and Longevity

We compiled a data set on freshwater mussel age and growth for 29 species from 70 populations (Table 2). The species included in this review represent the following genera: *Amblema*, *Fusconaia, Glebula*, *Lampsilis*, *Lasmigona*, *Leaunio*, *Megalonaias*, *Obliquaria*, *Plectomerus*, *Pleurobema*, *Potamilus*, *Pustulosa*, *Pyganodon*, *Quadrula*, *Toxolasma*, and *Truncilla* within the tribes Amblemini, Lampsilini, Pleurobemini, and Quadrulini, and represent a little over half of the species known to occur within Texas. Within this review we found that K ranges from 0.04 yr^{-1} (*Fusconaia flava*, Mountain Fork River, Arkansas; Sansom et al. 2016) and 0.04 (*Megalonaias nervosa*, St. Francis River, Arkansas; Christian et al. 2000) to 1.01 yr^{-1} (*Toxolasma parvum*, Davis Lake, Mississippi; Haag and Rypel 2011) and L_∞ ranges from

Table 2. Summary of (median or mean) growth parameter information for species of freshwater mussel known to occur in Texas. L_∞ = predicted mean maximal length for the population; K = Brody growth constant; t_0 = theoretical time at which $L = 0$; $A_{\max}$ = maximum observed age; $L_{\max}$ = measured maximum length; and N = number of individuals.

Species	Site	K	L_∞	t_0	$A_{\max}$	$L_{\max}$	N	Source
Amblema plicata	Little Tallahatchie River, MS	0.21	109	0.75	18	101.3	37	Haag and Rypel 2011
A. plicata	Sipsey River, AL	0.07	109.2	−0.34	54	114.7	11	Haag and Rypel 2011
A. plicata	White River, AR	0.09	138	0.83	25		22	Christian et al. 2000
A. plicata	Ouachita River, AR	0.13	87	−0.34	25		50	Christian et al. 2000
A. plicata	Guadalupe River, TX	0.12	92.4	−2.29	13		6	DuBose et al. 2022
A. plicata	Colorado River, TX	0.18	99.9	−0.97	23		9	DuBose et al. 2022
A. plicata	Amite River, LA	0.11			39	122.3	77	Daniel and Brown 2014
Fusconaia askewi	Village Creek, TX	0.19	56.81	−0.74	21		9	This study
Fusconaia flava	Little River, AR	0.06	92.11		29		3	Sansom et al. 2016
F. flava	Mountain Fork River, AR	0.04	89.16		64		3	Sansom et al. 2016
F. flava	Mulberry River, AR	0.26	74.9	−1.12			25	Stoeckel et al. 1996
Fusconaia mitchelli	Guadalupe River, TX	0.23	56.43	−0.12	15		54	Dudding et al. 2020
Glebula rotundata	Amite River, LA	0.05			34	164.5	69	Daniel and Brown 2014
Lampsilis bracteata	Llano River, TX	0.19	61.4	−0.19	13		24	de Moulpied et al. 2024
L. bracteata	San Saba River, TX	0.21	61.52	−0.13	12		24	de Moulpied et al. 2024
Lampsilis cardium	Iroquois River, IL	0.21	131.6	−1.72	10		8	DuBose et al. 2022
L. cardium	Mississippi River, MN	0.65	104.8	−1.64	10		1	DuBose et al. 2022
L. cardium	Mississippi River, MN	0.44	106.2	−1	13		3	DuBose et al. 2022
Lampsilis hydiana	Mulberry River, AR	0.47	83	0.64			70	Stoeckel et al. 1996
L. teres	Sipsey River, AL	0.41	108.2	0.34			7	Haag and Rypel 2011
Lampsilis teres	Sabine River, TX	0.34	139.78	0.39	13		9	This study
L. teres	St. Francis River, AR	0.57	132.8	0.61			22	Haag and Rypel 2011
L. teres	Amite River, LA	0.32			14	121.7	66	Daniel and Brown 2014
Lasmigona complanata	Ontario, Canada; grassy		136.59				40	Morris and Corkum 1999
L. complanata	Ontario, Canada; forested		153.61				45	Morris and Corkum 1999
Leaunio lienosus	Amite River, LA	0.21			20	77.0	89	Daniel and Brown 2014
L. lienosus	Kettle Creek, MS	0.40	70.1	0.18	11	72.4	6	Haag and Rypel 2011
L. lienosus	Sipsey River, AL	0.78	49.8	0.50	5	54.3	8	Haag and Rypel 2011
Megalonaias nervosa	Sipsey River, AL	0.09	165.8	−1.50	38	168.3	3	Haag and Rypel 2011
M. nervosa	St. Francis River, AR	0.04	217.8	−14.33	41		48	Christian et al. 2000
M. nervosa	Cache River, AR	0.08	239.2	−1.07	43		38	Christian et al. 2000
Obliquaria reflexa	Licking River, KY	0.37	55.1	0.55	15	60.9	15	Haag and Rypel 2011
O. reflexa (female)	Sipsey River, AL	0.16	50.7	−0.72	23	54	12	Haag and Rypel 2011
O. reflexa (male)	Sipsey River, AL	0.25	50.7	0.23	21	53	17	Haag and Rypel 2011
O. reflexa	Amite River, LA	0.23			19	59.6	89	Daniel and Brown 2014
Plectomerus dombeyanus	Amite River, LA	0.27					99	Daniel and Brown 2014
P. dombeyanus	Leaf River, MS	0.26	125	0.46	17	134	10	Haag and Rypel 2011
P. dombeyanus	Pearl River, MS	0.15	136.9	−1.88	38	144.5	8	Haag and Rypel 2011
Pleurobema riddellii	Neches River, TX	0.11	69.9			60.9	55	Ford et al. 2020
P. riddellii	LVNA Canal, TX	0.16	59.53	−1.26	18		14	This study
Potamilus fragilis	Licking River, KY	0.60	98.9	0.40	7	119.3	10	Haag and Rypel 2011
P. fragilis	St. Francis River, AR	0.72	141	0.19	4	137	115	Haag and Rypel 2011

Table 2, continued.

Species	Site	K	L_∞	t_0	$A_{\max}$	$L_{\max}$	N	Source
Potamilus purpuratus (male)	St. Francis River, AR	0.81	148.1	1.16	10	149.3	4	Haag and Rypel 2011
P. purpuratus (female)	St. Francis River, AR	0.49	120	0.25	9	129.4	15	Haag and Rypel 2011
P. purpuratus	Amite River, LA	0.08			32	204.3	76	Daniel and Brown 2014
Pustulosa necki	Guadalupe River, TX	0.14	55.49	−1.64	13		54	Dudding et al. 2020
Pustulosa nodulata	LNVA Canal, TX	0.21	48.60	−0.43	15		15	This study
Pustulosa petrina	Colorado River, TX	0.07	94.43	−2.18	22		16	de Moulpied et al. 2024
P. petrina	Llano River, TX	0.09	76.44	−1.5	17		19	de Moulpied et al. 2024
P. petrina	San Saba River, TX	0.10	55.03	−1.98	29		16	de Moulpied et al. 2024
Pustulosa pustulosa	Sabine River, TX	0.13	65.91	−1.41	26		15	This study
P. pustulosa	LVNA Canal, TX	0.13	56.85	−1.42	20		15	This study
P. pustulosa	Licking River, KY	0.14	86.2	0.37	39	88.2	17	Haag and Rypel 2011
P. pustulosa	Little Tallahatchie River, MS	0.08	72.4	−2.88	48	79.8	174	Haag and Rypel 2011
Pyganodon grandis	Kettle Creek, MS	0.31	123.2	0.03	9	127.5	9	Haag and Rypel 2011
P. grandis	Pearl River, MS	0.66	129	0.62	11	134.4	9	Haag and Rypel 2011
P. grandis	Wabana Lake, MN	0.03	112.0				55	Anthony et al. 2001
P. grandis	Narrow Lake, AB	0.26	74.2	0.94	12	75	618	Hanson et al. 1988
P. grandis	Ontario, Canada		135.13				200	Morris and Corkum 1999
Quadrula quadrula	LNVA Canal, TX	0.16	53.02	−1.02	16		10	This study
Q. quadrula	Ozark Lake, AR	0.10	120	−0.03	17		49	Christian et al. 2000
Q. quadrula	Lake Dardenelle, AR	0.90	99.4	−0.88	24		49	Christian et al. 2000
Quadrula verrucosa (male)	Sipsey River, AL	0.15	104.1	0.34	37	107.4	19	Haag and Rypel 2011
Q. verrucosa (female)	Sipsey River, AL	0.13	127.8	1.14	21	117.1	7	Haag and Rypel 2011
Q. verrucosa	Little River, AR	0.11	125.44		15		3	Sansom et al. 2016
Q. verrucosa	Little River, AR	0.10	111.67		34		4	Sansom et al. 2016
Toxolasma parvum	Davis Lake, MS	1.01	24	0.02	5	26.7	15	Haag and Rypel 2011
Toxolasma texasiense (male)	Kettle Creek, MS	0.56	42.3	0.18	8	43.7	5	Haag and Rypel 2011
T. texasiense (female)	Kettle Creek, MS	0.29	35.7	−0.56	11	35.8	2	Haag and Rypel 2011
Truncilla donaciformis	Licking River, KY	0.46	40.3	0.29	8	46.8	14	Haag and Rypel 2011
T. donaciformis	LNVA Canal, TX	0.25	41.19	−0.26	10		10	This study
Truncilla macrodon	Brazos River, TX	0.20	57.82	−0.41	10		22	This study
Truncilla truncata	Licking River, KY	0.24	65.8	0.05	10	65.3	14	Haag and Rypel 2011
T. truncata	St. Croix River, MN	0.16	50.2	−0.53	18	50.6	3	Haag and Rypel 2011

24 mm (*To. parvum*, Davis Lake, Mississippi; Haag and Rypel 2011) to 239.20 mm (*M. nervosa*, Cache River, Arkansas; Christian et al. 2000).

All tribes represented in our review showed considerable variation in longevity. Maximum observed age for Quadrulini ranged from 13 yr (*Pu. necki*, Guadalupe River, Texas; Dudding et al. 2020) to 48 yr (*Pu. pustulosa*, Little Tallahatchie River, Mississippi; Haag and Rypel 2011). Pleurobemini age had the most variability and ranged from 15 yr (*F. mitchellii*, Guadalupe River, Texas; Dudding et al. 2020) to 64 yr (*F. flava*, Mountain Fork, Arkansas; Sansom et al. 2016). The only Amblemini species reviewed was *A. plicata*, which had a reported observed age range of 13 yr (Guadalupe River, Texas; DuBose et al. 2022) to 54 yr (Sipsey River, Alabama; Haag and Rypel 2011). Maximum observed age for the Lampsilini tribe ranged from 5 yr (*Leaunio lienosus*, Sipsey River, Alabama and *To. parvum*, Davis Lake, Mississippi; Haag and Rypel 2011) to 23 yr (*Obliquaria reflexa*, Licking River, Kentucky; Haag and Rypel 2011).

The Brody growth constant, K, also showed considerable variation between and within the four tribes represented by this data set. Pleurobemini had the smallest range and the lowest K values of the four tribes, ranging from 0.04 yr^{-1} (*F. flava*) to 0.11 yr^{-1} (*Pl. riddellii*). It is worth noting that *F. flava* has also been reported to have a much higher K value of 0.26 yr^{-1} (Stoeckel et al. 1996). Next fastest was Quadrulini, which ranged from 0.04 yr^{-1} (*M. nervosa*) to 0.90 yr^{-1} (*Q. quadrula*). Only one Amblemini species was reviewed as part of this study, *A. plicata*, with a *K* value range of 0.07 yr^{-1} to 0.21 yr^{-1}. Lampsilini had both the highest growth constant and widest range, from 0.05 yr^{-1} (*Glebula rotundata*) to 1.01 yr^{-1} (*To. parvum*).

DISCUSSION

In this study we provided growth parameters for eight mussel species across four rivers in Texas. Of the species we evaluated, three previously lacked information on age and growth and four had estimates for populations outside of the state. Further, three of the species are of conservation concern (*F. askewi*, *Pl. riddellii*, and *Tr. macrodon*). Brody growth constants were highly variable, showing a gradient of growth rates and lifespans that generally can be correlated to fast and slow end points of the *r/K* continuum for unionids. Last, we compiled age and growth information for 29 species using original data and literature reports.

We found that age and growth varied across species and observed that species with smaller growth constants had higher maximum observed ages. This corroborates findings from previous studies (i.e., Haag and Rypel 2011) and suggests that growth constants serve as a good proxy for position along the *r/K* continuum. For example, in this study *Pu. pustulosa* had the lowest growth constant, 0.13 yr^{-1}, and was the longest-lived (20 to 26 yr) species we examined on the basis of maximum observed age. In contrast, *La. teres* had the highest growth, 0.34 yr^{-1}, more than double that of *Pu. pustulosa,* and was among the shortest-lived (13 yr) of the species we examined. Taken together, this would indicate that *Pu. pustulosa* is likely a slow or *K*-selected species, and should have higher fitness in stable, productive habitats, and *La. teres* is likely a fast or *r*-selected species and is adapted to rapid colonization and persistence in disturbed and unstable habitats (Haag 2012). Similarly, *Tr. donaciformis* is also likely an *r*-selected species with high growth (0.25 yr^{-1}) and short lifespan (10 yr; Haag and Rypel 2011; Haag 2012). For *Q. quadrula*, *Pl. riddellii*, and *F. askewi*, growth constants suggest they are likely positioned near the *K* end point, whereas *Pu. nodulata* and *Tr. macrodon* likely fall near the *r* end point.

We found that maximum observed age and the growth constant did not vary among populations for *Pu. pustulosa*, which is not unexpected given the geographic proximity and similarity in climate between sample locations. Nearly identical growth parameters were found for *La. bracteata* (Texas fatmucket) from the Llano and San Saba rivers of the Colorado River basin, which are close together (de Moulpied et al. 2024). In a review of age and growth for mussels in North America, similar growth estimates were noted between populations in the same river system for several species (Haag and Rypel 2011). Both studies also found instances where *K* varied among populations of the same species. For example, *K* varied across three populations of *Pustulosa petrina* (Texas pimpleback) in three different river systems in the Colorado River basin (de Moulpied et al. 2024). The authors hypothesized that the variation in *K* could be the result of differences in extreme flooding between sample locations. Similarly, *Quadrula asperata*, now *Pustulosa kieneriana*, had differences in *K* for different populations, suggesting the differences represent alternative fitness-maximizing life-history strategies (Haag and Rypel 2011). Taken together, these findings indicate that growth parameters are not always portable across populations even if they are near one another, and they also suggest that differences may arise because of local disturbances or polymorphisms that represent divergent life histories (Haag and Rypel 2011; Sansom et al. 2016).

Our estimates of longevity and growth were different across phylogenetic groups, corresponding with differences in life history. Specifically, we found that, on average, species in the Lampsilini tribe had the highest *K* value, followed by Pleurobemini and then Quadrulini. Variation in longevity across the three tribes follows a similar pattern such that species in the Lampsilini tribe have shorter lifespans compared with species in Pleurobemini and Quadrulini (Haag and Rypel 2011). According to *r/K* theory, species with fast growth and short lifespans are expected to occur in more variable environments compared with species with slower growth that are long lived (Pianka 1970; Haag 2012). These relationships suggest that age and growth are broadly constrained by phylogeny (Haag and Rypel 2011), which is not unexpected given that other traits also show the same patterns. For example, Quadrulini species generally reach maturity later, have lower fecundity, and use a broadcasting strategy to infect host fish with their larvae (Haag 2012; Neemuchwala et al. 2023), whereas Lampsilini species generally mature young, have higher fecundity, and use lures to attract a specific fish (Barnhart et al. 2008; Haag 2012).

Although we successfully estimated growth parameters for eight species in East Texas, 41 species have yet to be evaluated within the state. The results of this study show that growth parameters may be transferable within species, but phenotypic plasticity does exist. Although this variation could complicate efforts to predict how species may respond to environmental change or specific management actions, a general understanding of whether a species is *r*- or *K*-selected can still guide managers in their decision-making. That said, more information is needed on age and growth within and across species—not just in Texas but for freshwater mussels everywhere. Research efforts should continue focusing on generating age and growth information but also validate those estimates using mark–recapture and statistical methods such as cross-dating (Rypel et al. 2008). These methods allow for the formation of long-term growth chronologies that can be used to validate new age estimates. Also, more information is needed on the relationships between growth and reproduction, which would facilitate the application of more complex life-history models. Future studies should focus on characterizing fecundity and age of maturation in conjunction with estimating age and growth. The former can be obtained by collecting gravid females and then enumerating the number of larvae (i.e., glochidia) following established protocols (e.g., Haag and Staton 2003).

Patterns of age and growth are fundamental to understanding species life history, which provides a framework for understanding how mussels may respond to environmental change or management and conservation actions (Hastie et al. 2000; Albaladejo-Robles et al. 2023). For example, species with high growth rates and reduced longevity are found more often in habitats that experience streambed disturbance during high-flow events compared with species with lower growth rates and longer lifespans. These associations have been used to develop a conceptual model (Randklev et al. 2019) to predict mussel assemblage structure on the basis of extreme flooding. The growth parameters we estimated for our eight focal species could be incorporated into this model to provide greater insight into how these species and others may respond to changes in the flow regime. This type of information is critical because future climate and land-use change in Texas may increase droughts and floods (Griffith et al. 2007; Jiang and Yang 2012; Nielsen-Gammon et al. 2020) and understanding how mussels respond to these events is critical for ensuring conservation strategies are tailored to the life history of target species.

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