

Growth and longevity in freshwater mussels: evolutionary and conservation implications

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(Received 31 December 2009; revised 2 June 2010; accepted 7 June 2010)

ABSTRACT

The amount of energy allocated to growth *versus* other functions is a fundamental feature of an organism's life history. Constraints on energy availability result in characteristic trade-offs among life-history traits and reflect strategies by which organisms adapt to their environments. Freshwater mussels are a diverse and imperiled component of aquatic ecosystems but little is known about their growth and longevity. Generalized depictions of freshwater mussels as 'long-lived and slow-growing' may give an unrealistically narrow view of life-history diversity which is incongruent with the taxonomic diversity of the group and can result in development of inappropriate conservation strategies. We investigated relationships among growth, longevity, and size in 57 species and 146 populations of freshwater mussels using original data and literature sources. In contrast to generalized depictions, longevity spanned nearly two orders of magnitude, ranging from 4 to 190 years, and the von Bertalanffy growth constant, K , spanned a similar range (0.02–1.01). Median longevity and K differed among phylogenetic groups but groups overlapped widely in these traits. Longevity, K , and size also varied among populations; in some cases, longevity and K differed between populations by a factor of two or more. Growth differed between sexes in some species and males typically reached larger sizes than females. In addition, a population of *Quadrula asperata* exhibited two distinctly different growth trajectories. Most individuals in this population had a low-to-moderate value of K (0.15) and intermediate longevity (27 years) but other individuals showed extremely slow growth ($K = 0.05$) and reached advanced ages (72 years). Overall, longevity was related negatively to the growth rate, K , and K explained a high percentage of variation in longevity. By contrast, size and relative shell mass (g mm^{-1} shell length) explained little variation in longevity. These patterns remained when data were corrected for phylogenetic relationships among species. Path analysis supported the conclusion that K was the most important factor influencing longevity both directly and indirectly through its effect on shell mass. The great variability in age and growth among and within species shows that allocation to growth is highly plastic in freshwater mussels. The strong negative relationship between growth and longevity suggests this is an important trade-off describing widely divergent life-history strategies. Although life-history strategies may be constrained somewhat by phylogeny, plasticity in growth among populations indicates that growth characteristics cannot be generalized within a species and management and conservation efforts should be based on data specific to a population of interest.

Key words: age, life history, growth rate, von Bertalanffy, Unionidae, Margaritiferidae, Unionoida.

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I. INTRODUCTION

The amount of energy invested in growth is an important feature of an organism's life history and is predicted to covary with investment in other life-history traits or functions including body size, survival, maintenance, reproduction, age at maturity, and longevity (Stearns, 1983). Nevertheless, patterns of investment in growth have been largely neglected in studies of life-history evolution (Arendt, 1997). Recent studies showing a negative relationship between growth and longevity (Bauer, 1992; Olsson & Shine, 2002; Rollo, 2002; Metcalfe & Monaghan, 2003) suggest that allocation to growth represents a critical life-history trade-off. Life-history trade-offs occur in predictable ways producing characteristic suites of life-history traits (Winemiller & Rose, 1992; Charnov, 1993; Grime, 1997). These divergent life histories reflect adaptive strategies for exploiting resources in different ways and in different habitats and are therefore important in generating and maintaining biological diversity (Schluter, 2000). In addition to their evolutionary significance, life-history strategies are important in conservation of exploited or imperiled species because life-history traits have direct bearing on how organisms respond to management or habitat alteration (Winemiller & Rose, 1992; Bennett & Owens, 1997).

Freshwater mussels (order Unionoida) are a diverse, conspicuous component of aquatic ecosystems. The North American fauna is the most diverse on Earth with about 300 species in two families (Margaritiferidae and Unionidae: Graf & Cummings, 2007; Bogan, 2008), and mussels often compose a high percentage of benthic biomass (Strayer *et al.*, 1999; Vaughn & Hakenkamp, 2001). Freshwater mussels are also a critically endangered group of organisms and are declining at some of the highest known rates on Earth (Regnier, Fontaine & Bouchet, 2009). Mussels are currently the focus of intensive conservation efforts but these efforts are severely hampered by a lack of life history information (e.g. Neves *et al.*, 1997). Age, growth, and longevity data are

especially critical in assessing the risk of extinction of rare and endangered species (Dennis, Munholland & Scott, 1991).

As a group, freshwater mussels are often portrayed as long-lived and slow-growing (e.g. Strayer *et al.*, 2004). This generalization is informed in large part by data from a single species, *Margaritifera margaritifera*, which grows slowly and reaches an age of 100–200 years (Bauer, 1992; Ziuganov *et al.*, 2000), but age and growth data exist for few other species. Although other mussel species are known to reach advanced ages (e.g. >50 years for *Elliptio crassidens*: Rypel, Haag & Findlay, 2008), many appear to grow more rapidly and have more modest life spans (e.g. 10 years for *Alasmidonta heterodon*: Michaelson & Neves, 1995; 12 years for *Pyganodon grandis*: Hanson, Mackay & Prepas, 1988). Consequently, the generalized and homogeneous depiction of freshwater mussels as 'long-lived and slow-growing' can result in an unrealistically narrow view of life-history diversity which is incongruent with the great taxonomic diversity of the group. Furthermore, conservation strategies developed under the assumption that mussels are slow-growing and long-lived will be inappropriate for species that do not conform to this generalization.

The lack of age and growth information for freshwater mussels is due in part to methodological issues associated with age determination. Freshwater mussels deposit conspicuous rings in their shells similar to annual growth rings in trees, fish scales and otoliths, marine bivalve shells, and hard structures in a wide variety of other organisms. Interpretation of age and growth data from shell rings has been hampered by debate over whether these rings represented annual growth increments (e.g. Strayer *et al.*, 2004). However, recent validation of annual ring production based on several independent methods and in a wide variety of species (reviewed in Haag, 2009) allows utilization of the wealth of information contained within freshwater mussel shells.

We examined patterns of growth and longevity in freshwater mussels, primarily from North America, using original data and literature reports. In our original data set,

the assumption of annual ring formation was assessed using dendrochronological cross-dating techniques. We used von Bertalanffy growth parameters and estimates of maximum size and age to investigate patterns of growth at several levels including among major phylogenetic groups (tribes and families), across species, among and within populations, and between sexes. We describe relationships among shell length and mass, growth rate (measured by the von Bertalanffy parameter, K), and longevity, and used phylogenetically independent contrasts to assess the degree to which these relationships are artifacts of phylogenetic relationships among species. We then used path analysis to investigate the relative contribution of shell size and mass and growth rate in explaining observed variation in longevity. We discuss the relevance of variation in growth and longevity to mussel conservation and life-history evolution.

II. METHODS

(1) The data set

We compiled a data set on freshwater mussel age and growth that included 57 species from 146 populations (Table 1). We generated original growth data from shell thin sections of 41 North American species from 69 populations in Alabama, Arkansas, Kentucky, Minnesota, and Mississippi. For each population, we examined a broad length range of individuals and, because we were interested in estimating maximum life span, we paid particular attention to obtaining the largest (and ostensibly, the oldest) individuals present as well as individuals with tightly crowded annuli. We excluded populations for which samples lacked older individuals (e.g. samples obtained exclusively from muskrat middens), but we included some populations with small sample sizes if the sample included specimens from the upper end of the size range present at the site. We also obtained age and growth data from the literature for 20 species and 77 populations, including six additional populations of four species represented in our original data set. We used data only from studies that directly estimated age and growth from shell or hinge-ligament annuli and did not include extrapolated age estimates based on predictions from von Bertalanffy or other growth models (e.g. Aldridge, 1999; Anthony *et al.*, 2001; Howard & Cuffey, 2006; see Haag, 2009). Most species in our combined data set are North American (54 species) and these species represent a broad cross section of North American mussel diversity including members of all major phylogenetic groups (Margaritiferidae, Unionidae: tribes Amblemini, Anodontini, Lampsilini, Pleurobemini, and Quadrolini; Campbell *et al.*, 2005, see Table 1). Our data set also included three European species from three major phylogenetic groups (Margaritiferidae, Unionidae: tribes Anodontini and Unionini); one of these species also occurs in North America (*Margaritifera margaritifera*).

For all populations we obtained estimates of von Bertalanffy growth parameters (K , L_{inf} , and t_0 , see Section II.5),

maximum observed age (A_{max} , years), and maximum observed length (L_{max} , mm), as available. If L_{max} was not reported we used L_{inf} as a measure of L_{max} . If von Bertalanffy equations were not reported, we estimated the parameters if length at age data were presented in the source.

(2) Shell mass

In addition to shell length, we were interested in evaluating how differences in shell mass among species were related to patterns of longevity and growth. Mussel species differ widely in the thickness of their shells and presumably in the amount of energy allocated to shell production. Furthermore, although total length may cease to increase perceptively as individuals near their growth asymptote, shell material continues to be deposited on the inner surface of the shell resulting in continued increases in shell mass with age (McMahon & Bogan, 2001). For this reason, shell mass may be more accurate than length for measuring continued investment in shell growth with age. Shell mass also may be related to longevity because the strength of the shell is probably important in resisting predation and mechanical damage (e.g. Vermeij, 1993).

We measured maximum shell mass for all populations in our original growth data set. For each population, we measured mass of one valve of the five largest specimens in our sample on an electronic balance (to nearest 0.01 g) and also recorded the length of each specimen (to nearest 0.1 mm). We then expressed mass as a ratio of \log_{10} mass/ \log_{10} length for each specimen and used the mean ratio to represent a relative measure of maximum investment in shell mass per unit size (relative shell mass, RM , g mm^{-1}) for each species. Shell mass was not reported for populations in literature sources, and we did not attempt to obtain shells from those populations. Furthermore, because relative shell mass can vary considerably among populations, we did not attempt to estimate mass of species from literature reports by using available shells from different populations. We did measure relative shell mass for two members of the family Margaritiferidae (*Cumberlandia monodonta* and *Margaritifera hembeli*) but used these measurements only for broad comparisons of variation among major taxonomic groups (see Fig. 1) and did not use these measurements for testing statistical relationships among growth variables (see Section II.5).

(3) Preparation and interpretation of shell thin sections

We prepared radial thin sections ($\sim 300 \mu\text{m}$ thickness) from one valve of each specimen using a low-speed saw with a diamond-impregnated blade (Buehler Ltd., Lake Bluff, IL, USA), following Haag & Commens-Carson (2008) and based on standard methods for bivalves (Clark, 1980; Neves & Moyer, 1988; Veinott & Cornett, 1996). All thin sections were interpreted independently by two experienced observers using a binocular microscope and transmitted light. We identified annual rings and differentiated them from non-annual shell rings (e.g. disturbance rings) following criteria described

Table 1. Age and growth data for freshwater mussels. The variables K , L_{inf} , and t_0 are parameters of the von Bertalanffy growth equation. A_{max} is maximum observed age (years); L_{max} is maximum observed length (mm), N is number of individuals. Superscripts after the data source for each population indicate the validation method used to test the assumption of annual formation of rings in shells or hinge ligaments as follows: (1) mark-recapture analysis of timing of shell ring deposition; (2) crossdating; (3) comparison of growth inferred from annuli with growth estimated from mark-recapture study; (4) validation reported previously for same species but from other populations; (5) no validation. *, von Bertalanffy parameters not reported but calculated by us using data presented in source; †, age estimated from hinge-ligament annuli; all other estimates are from shell annuli; —, not given. For literature studies with >2 populations, we give ranges of values for each variable. Sex-specific growth data are given separately only for species for which at least one parameter differed significantly between sexes (see Section III.4.a). For *Quadrula asperata*, growth data are given separately for the two growth forms ('normal' and 'slow') that we observed in one population (Sipsey River, AL, site 1; see Section III.4.b)

Species	Site	K	L_{inf}	t_0	A_{max}	L_{max}	N	Source
Family Margaritiferidae								
<i>Cumberlandia monodonta</i> †	Gasconade and Meramec Rivers, MO	—	—	—	56	—	278	Baird (2000) ³
<i>Margaritifera falcata</i> †	Madison River, MT	—	—	—	67	—	84	Stober (1972) ⁵
<i>M. falcata</i>	Salmon River, ID	—	—	—	100	161.0	—	Vannote & Minshall (1982) ⁵
<i>Margaritifera margaritifera</i> †	11 populations, Scotland	0.023–0.081	77–158	–3.93–4.33	48–123	105–150	22–93	Hastie <i>et al.</i> (2000) ⁴
<i>M. margaritifera</i>	Three populations, Russian arctic	—	—	—	114–190	120–162	13–44	Ziuganov <i>et al.</i> (2000) ⁴
<i>M. margaritifera</i>	Two populations, Sakhalin and Kuril Islands	—	—	—	28–32	123–136	13–23	Ziuganov <i>et al.</i> (2000) ⁴
<i>M. margaritifera</i>	Six populations, Spain	—	—	—	32–40	92.5–111.3	9–26	Ziuganov <i>et al.</i> (2000) ⁴
<i>M. margaritifera</i>	16 populations, Spain	0.089–0.144	80.0–102.0	–0.397–1.613	35–65	91.0–117.0	12–52	San Miguel <i>et al.</i> (2004) ⁴
Family Unionidae								
Tribe Amblemini								
<i>Amblema plicata</i>	Little Tallahatchie River, MS	0.207	109.0	0.747	18	101.3	37	this study ^{1,2}
<i>A. plicata</i>	Sipsey River, AL	0.074	109.2	–0.340	54	114.7	11	this study ²
<i>A. plicata</i>	White River, AR	0.090	138.0	0.830	25	—	22	Christian <i>et al.</i> (2000) ⁵
<i>A. plicata</i>	Ouachita River, AR	0.130	87.0	–0.340	25	—	50	Christian <i>et al.</i> (2000) ⁵
Tribe Anodontini								
<i>Alasmidonta heterodon</i>	Aquia Creek, VA	0.260	45.3	0.244	9	43.8	40	Michaelson & Neves (1995) ⁵
<i>A. heterodon</i>	Neversink River, NY	0.207	46.8	0.335	10	42.6	21	Michaelson & Neves (1995) ⁵
<i>Alasmidonta marginata</i>	Licking River, KY	0.439	84.4	0.316	7	84.8	16	this study ²
<i>Alasmidonta viridis</i>	Brushy Creek, KY	0.417	34.6	–0.290	18	37.4	7	this study ²
<i>Anodonta piscinalis</i> *	Two populations, Finland	0.318	115.9	0.490	8	—	100	Haukioja & Hakala (1978) ¹
<i>Lasnigona costata</i>	Licking River, KY	0.250	133.9	0.049	19	140.6	10	this study ²
<i>Pyganodon grandis</i>	Kettle Creek, MS	0.314	123.2	0.031	9	127.5	9	this study ²
<i>P. grandis</i>	Pearl River, MS	0.659	129.0	0.619	11	134.4	9	this study ²
<i>P. grandis</i> *	Narrow Lake, AB	0.261	74.2	0.943	12	75.0	618	Hanson <i>et al.</i> (1988) ⁴
<i>Strophitus subvexus</i>	Shoal Creek, AL	0.215	96.2	0.403	18	94.6	11	this study ²
Tribe Lampsilini								
<i>Actinonaias ligamentina</i>	Green River, KY	—	—	—	~50	—	—	Moles & Layzer (2008) ¹
<i>A. ligamentina</i> *	Seven populations, central North America	0.077–0.173	107.8–161.3	–0.292–0.708	22–40	116.0–175.0	55–120	St. John (1973) ³

Table 1. (Cont.)

Species	Site	K	L_{-inf}	t_0	A_{max}	L_{max}	N	Source
<i>Cyprogenia aberti</i>	Spring River, AR	0.292	51.9	0.299	14	52.6	16	this study ²
<i>Cyprogenia stegaria</i>	Licking River, KY	0.183	74.4	0.260	20	74.7	29	this study ²
<i>C. stegaria</i>	Clinch River, TN	0.146	53.2	-0.053	26	56.0	84	Jones & Neves (2002) ⁵
<i>Dromus dromas</i>	Clinch River, TN	0.123	70.1	-0.111	25	78.4	66	Jones <i>et al.</i> (2004) ⁵
<i>Elptisaria lineolata</i> (female only)	Tennessee River, AL	0.232	64.4	-0.879	19	65.6	18	this study ²
<i>Epioblasma penita</i>	Buttahatchee River, MS	0.291	49.0	-0.252	9	52.7	7	this study ²
<i>Haniota althlis</i>	Shoal Creek, AL	0.242	63.3	-0.558	15	65.0	15	this study ²
<i>Lampsilis ornata</i>	Sipsey River, AL	0.382	82.0	-0.364	18	95.4	29	this study ^{1,2}
<i>Lampsilis straminea</i>	Sipsey River, AL	0.270	79.3	-0.084	25	88.3	13	this study ²
<i>Lampsilis teres</i>	Sipsey River, AL	0.410	108.2	0.336	13	108.1	7	this study ²
<i>L. teres</i>	St. Francis River, AR	0.569	132.8	0.609	13	143.0	22	this study ^{1,2}
<i>Leptodea fragilis</i>	Licking River, KY	0.597	98.9	0.399	7	119.3	10	this study ²
<i>L. fragilis</i>	St. Francis River, AR	0.720	141.0	0.193	4	137.0	115	this study ^{1,2}
<i>Ligumia recta</i>	St. Croix River, MN	0.257	134.1	0.534	16	144.0	9	this study ²
<i>L. recta</i>	Tennessee River, AL	0.639	150.5	1.015	10	154.0	3	this study ²
<i>Medionidus acutissimus</i>	Sipsey River, AL	0.637	31.9	0.363	5	34.1	29	this study ²
<i>Obliquaria reflexa</i>	Licking River, KY	0.365	55.1	0.548	15	60.9	15	this study ²
<i>O. reflexa</i> (female)	Sipsey River, AL	0.158	50.7	-0.720	23	54.0	12	this study ^{1,2}
<i>O. reflexa</i> (male)	Sipsey River, AL	0.247	50.7	0.232	21	53.0	17	this study ^{1,2}
<i>Obovaria jacksoniana</i> (female)	Sipsey River, AL	0.164	35.3	-1.350	14	34.0	12	this study ²
<i>O. jacksoniana</i> (male)	Sipsey River, AL	0.146	45.3	-1.300	34	50.4	14	this study ²
<i>Obocaria unicolor</i> (female)	Sipsey River, AL	0.192	39.8	-1.044	20	41.9	16	this study ²
<i>O. unicolor</i> (male)	Sipsey River, AL	0.117	49.7	-3.356	44	50.2	29	this study ²
<i>Potamilus purpuratus</i> (female)	St. Francis River, AR	0.490	120.0	0.250	9	129.4	15	this study ^{1,2}
<i>P. purpuratus</i> (male)	St. Francis River, AR	0.813	148.1	1.161	10	149.3	4	this study ^{1,2}
<i>P. purpuratus</i> (male)	Pearl River, MS	0.321	160.7	-0.243	26	194.5	9	this study ²
<i>Psychobranchus fasciolaris</i>	Licking River, KY	0.103	149.6	-1.108	32	157.4	4	this study ²
<i>Toxolasma parva</i>	Davis Lake, MS	1.008	24.0	0.018	5	26.7	15	this study ²
<i>Toxolasma pulbus</i>	University Lake, NC	—	—	—	9	—	40	Hanlon & Levine (2004) ⁵
<i>Toxolasma texasensis</i> (male)	Kettle Creek, MS	0.556	42.3	0.182	8	43.7	5	this study ²
<i>T. texasensis</i> (female)	Kettle Creek, MS	0.288	35.7	-0.557	11	35.8	2	this study ²
<i>Truncilla donaciformis</i>	Licking River, KY	0.456	40.3	0.288	8	46.8	14	this study ²
<i>Truncilla truncata</i>	Licking River, KY	0.240	65.8	0.049	10	65.3	14	this study ²
<i>T. truncata</i>	St. Croix River, MN	0.157	50.2	-0.530	18	50.6	3	this study ²
<i>Villosa benosa</i>	Kettle Creek, MS	0.387	70.1	0.184	11	72.4	6	this study ²
<i>V. benosa</i>	Sipsey River, AL	0.782	49.8	0.499	5	54.3	8	this study ²
<i>Villosa nebulosa</i> (female)	Shoal Creek, AL	0.477	45.0	-0.038	6	44.0	11	this study ²
<i>V. nebulosa</i> (male)	Shoal Creek, AL	0.232	63.9	-0.321	12	60.4	11	this study ²
<i>Villosa vibex</i> (female)	Shoal Creek, AL	0.405	55.9	-0.201	7	60.4	7	this study ²
<i>V. vibex</i> (male)	Shoal Creek, AL	0.340	67.8	0.013	12	79.2	24	this study ²
Tribe Pleurobemini								
<i>Elptisio arca</i>	Buttahatchee River, MS	0.251	77.0	-0.372	34	79.5	13	this study ²
<i>E. arca</i>	Sipsey River, AL (site 1)	0.219	78.7	-0.128	32	88.3	81	this study ^{1,2}

Table 1. (Cont.)

Species	Site	k	L_{inf}	t_0	A_{max}	L_{max}	N	Source
<i>E. arca</i>	Sipsey River, AL (site 2)	0.309	80.3	0.160	14	83.3	11	this study ^{1,2}
<i>Elitipho complanata</i>	Mirror Lake, NH	—	—	—	16	71.0	—	Strayer <i>et al.</i> (1981) ⁵
<i>E. complanata</i>	Morice Lake, NB	—	—	—	15	82.0	416	Paterson (1985) ⁵
<i>Elitipho crassidens</i>	Buttahatchee River, MS	0.165	109.5	-0.351	44	114.0	5	this study ²
<i>E. crassidens</i>	Sipsey River, AL	0.118	114.5	-1.483	57	127.7	21	this study ²
<i>Fusconaita cerina</i>	Buttahatchee River, MS	0.235	55.8	-0.056	15	62.2	15	this study ²
<i>F. cerina</i>	Sipsey River, AL	0.173	55.4	-0.314	45	61.6	44	this study ^{1,2}
<i>Fusconaita cancolus</i>	Clinch River, VA (site 1)	0.130	80.0	0.050	32	80.2	—	Bruenderman & Neves (1993) ⁵
<i>F. cancolus</i>	Clinch River, VA (site 2)	0.080	91.3	0.031	30	—	—	Bruenderman & Neves (1993) ⁵
<i>Fusconaita ebena</i>	White River, AR	0.130	115.9	2.090	26	—	52	Christian <i>et al.</i> (2000) ⁵
<i>F. ebena</i>	Black River, AR	0.140	102.2	0.410	51	—	39	Christian <i>et al.</i> (2000) ⁵
<i>Platrobema coccineum</i>	Licking River, KY	0.134	96.9	-0.299	30	104.5	11	this study ²
<i>Platrobema collina</i>	John's Creek, VA	0.116	74.4	1.244	19	75.2	100	Hove & Neves (1994) ¹
<i>Platrobema decisum</i>	Sipsey River, AL	0.145	61.0	-0.331	45	67.0	45	this study ²
Tribe Quadrulini								
<i>Cyclonaias tuberculata</i>	New River, WV (three populations)	0.110–0.164	87.0–113.9	0.000–1.140	36–61	95.0–123.0	17–20	Jirka (1986) ⁵
<i>C. tuberculata</i>	Greenbrier River, WV	0.094	90.6	0.100	91	112.0	25	Jirka (1986) ⁵
<i>Megaloniais nervosa</i>	Sipsey River, AL	0.092	165.8	-1.504	38	168.3	3	this study ²
<i>M. nervosa</i>	St. Francis River, AR	0.040	217.8	-14.330	41	—	48	Christian <i>et al.</i> (2000) ⁵
<i>M. nervosa</i>	Cache River, AR	0.080	239.2	-1.070	43	—	38	Christian <i>et al.</i> (2000) ⁵
<i>Quadrula asperata</i>	Buttahatchee River, MS	0.187	53.1	1.255	21	53.8	45	this study ²
<i>Q. asperata</i> (normal)	Sipsey River, AL (site 1)	0.152	53.1	-0.161	27	56.2	39	this study ^{1,2}
<i>Q. asperata</i> (slow)	Sipsey River, AL (site 1)	0.050	52.1	-5.221	72	54.5	10	this study ^{1,2}
<i>Q. asperata</i>	Sipsey River, AL (site 2)	0.220	51.4	0.139	19	52.6	41	this study ^{1,2}
<i>Q. asperata</i>	Sipsey River, AL (site 3)	0.177	50.6	-0.904	20	53.2	78	this study ^{1,2}
<i>Q. asperata</i>	Tombigbee River, MS	0.299	68.9	0.095	15	71.7	18	this study ²
<i>Quadrula pustulosa</i>	Licking River, KY	0.143	86.2	0.369	39	88.2	17	this study ²
<i>Q. pustulosa</i>	Little Tallahatchie River, MS	0.076	72.4	-2.877	48	79.8	174	this study ^{1,2}
<i>Quadrula quadrula</i>	Ozark Lake, AR	0.100	120.0	-0.030	17	—	49	Christian <i>et al.</i> (2000) ⁵
<i>Q. quadrula</i>	Lake Dardenelle, AR	0.090	99.4	-0.880	24	—	49	Christian <i>et al.</i> (2000) ⁵
<i>Quadrula refulgens</i>	Pearl River, MS	0.194	48.5	-0.799	33	52.5	15	this study ²
<i>Quadrula rumphiana</i>	Sipsey River, AL	0.167	59.7	0.049	28	71.2	30	this study ^{1,2}
<i>Quadrula verrucosa</i> (female)	Sipsey River, AL	0.126	127.8	1.141	21	117.1	7	this study ^{1,2}
<i>Q. verrucosa</i> (male)	Sipsey River, AL	0.152	104.1	0.344	37	107.4	19	this study ^{1,2}
tribe Unionini								
<i>Unio terminalis</i>	Lake Kinneret, Israel (site 1)	0.412	52.4	—	10	—	100	Ostrovsky <i>et al.</i> (1993) ⁵
<i>U. terminalis</i>	Lake Kinneret, Israel (site 2)	0.323	53.0	—	10	—	146	Ostrovsky <i>et al.</i> (1993) ⁵
Unionidae, incertae sedis								
<i>Conidea angulata</i>	Salmon River, ID	—	—	—	24	110.0	—	Vannote & Minshall (1982) ⁵
<i>Plectomerus dombeyanus</i>	Leaf River, MS	0.264	125.0	0.457	17	134.0	10	this study ²
<i>P. dombeyanus</i>	Pearl River, MS	0.149	136.9	-1.879	38	144.5	8	this study ²

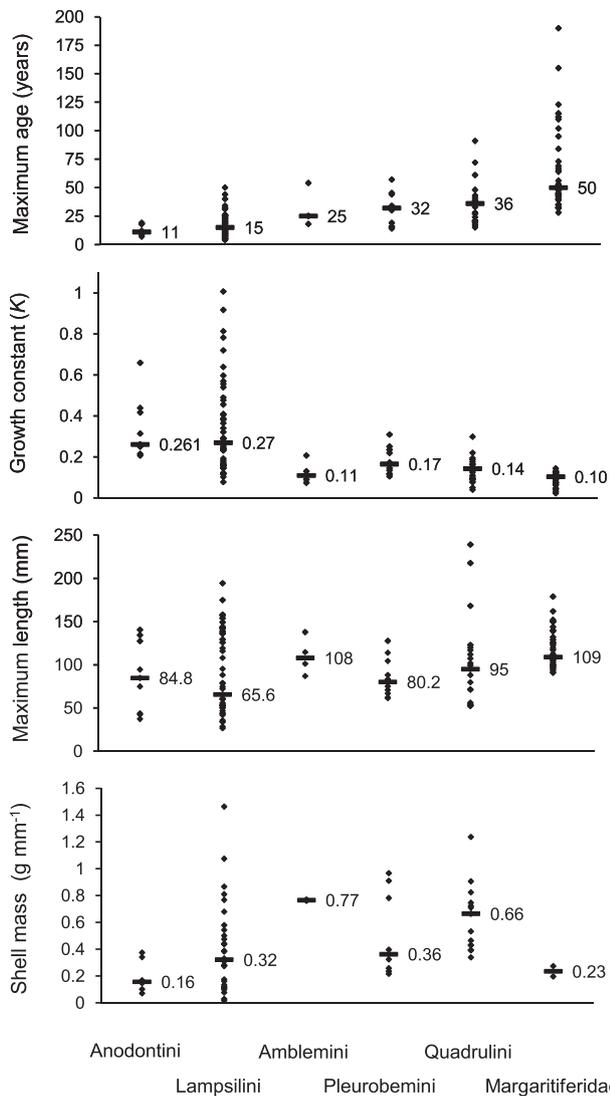


Fig. 1. Phylogenetic patterns of age and growth for freshwater mussels of the order Unionoida. Numbers represent median values for each phylogenetic group. The tribe Unionini was not included due to small sample size in our data set.

by Haag & Commens-Carson (2008). If the two observers differed in their interpretation of a shell and could not reach consensus following re-examination of the specimen, the specimen was excluded from further analysis. For each specimen, we marked consensus annuli on thin sections and counted them to estimate age, and measured the total shell length with dial calipers (greatest anterior-posterior dimension, to nearest 0.1 mm). For specimens with erosion of the umbo, we estimated the number of missing rings based on length at age data for the species at that site (e.g. Hastie, Boon & Young, 2000).

In addition to length at age at the time of collection, bivalve shells provide a growth record that in many cases spans the life of an individual. To extract this information we back-measured shell length at all interpretable annuli for most specimens (Aldridge, 1999; Michaelson & Neves, 1995).

Annuli were located on the shell surface by juxtaposing the marked thin section with the cut half of the shell, then transferring these marks to the shell (Michaelson & Neves, 1995; Haag & Commens-Carson, 2008). These marks were then transferred to the uncut shell valve and total length was measured at each annulus; in most cases, annuli identified in thin sections were also represented by visible annuli on the shell surface. On older specimens, the first few annuli were often obliterated by shell erosion and it was also usually possible to measure length only up to about age 10 years because the highly crowded nature of later annuli made them difficult to locate with precision on the shell surface. Back-measuring provided juvenile length at age data in species for which young individuals were unavailable; this information was important because the accuracy of von Bertalanffy growth equations is highly dependent on having growth data for all age classes (Haag, 2009).

For specimens collected alive, we accounted for time of collection by expressing final age as a decimal year based on month of collection and using January 1 as birth date (e.g. a nine-year-old specimen collected in May had a total age of 9.42). This adjustment was potentially important in correcting for variability in size of young or fast-growing specimens that were collected at different dates but was probably unimportant for older or slow-growing specimens. Expressing age as a decimal year also allowed us to include specimens that were less than one year old. For young or fast-growing specimens that were collected as recently dead shells (for which month of death was unknown), we measured size at all interpretable annuli up to the year before death, but did not include growth in the final year. We did measure final size and age for old and slow-growing specimens (greater than about 10 years old) because discrepancies caused by variation in time of death would have been minimal.

(4) Validation of growth increments

Literature sources varied in their attempts to validate putative annual rings and ranged from papers with no validation to those that validated annual rings with some care (see Table 1). The assumption of annual formation of shell rings was validated previously for 23 populations in our original data set (Haag & Commens-Carson, 2008; Rypel *et al.*, 2008; see Table 1). We used cross-dating to test the hypothesis of annual shell ring formation in 42 populations in our original data set that had not been validated previously. In this analysis, we combined sexes for all species and excluded individuals less than three years old because young specimens cannot produce a useful growth time-series.

Cross-dating followed the methods of Rypel *et al.* (2008) and was carried out with the dendrochronology program, COFECHA (Holmes, 1983; Grissino-Mayer, 2001). Briefly, we measured all interpretable growth increments (to nearest 0.1 mm) for each specimen and removed age-related variation to produce a standardized growth chronology. We constructed a master growth chronology for each species by computing the average standardized growth increment for each year across all specimens. We then correlated

the chronology of each specimen with an adjusted master chronology created by omitting the series of that particular individual (Grissino-Mayer, 2001), and calculated a mean interseries correlation coefficient across all individuals. Mean interseries correlations were used to assess the overall robustness of the annual growth pattern for each population; high correlations indicate strong growth synchrony among individuals.

As a quality-control technique we lagged each measurement time series forward and backward incrementally by 1–3 years and correlated lagged series with the master chronology (Grissino-Mayer, 2001). If the correlation coefficient was strongest with the series in its original placement in time, we considered that the shell thin section had been interpreted correctly (Holmes, 1983). If correlation coefficients were stronger after lagging, we re-examined the specimen for potential errors in interpretation (e.g. missed annual rings, nonannual rings counted as annual) or measurement errors. Deviations from the master chronology could also reflect individual variation in growth due to disturbance or other random factors (Grissino-Mayer, 2001). Therefore, if no obvious interpretative errors were found, we retained the specimen in the data set with its original measurements.

After cross-dating, we examined the periodicity of ring formation. First, we constructed a detrended master growth chronology for each population using the dendrochronology program ARSTAN (Cook & Holmes, 1984) to maximize climate-related variation. Then, we correlated annual variation in growth as reflected in master chronologies with mean streamflow for each year in our observed growth time series (see Table 2). Flow data were obtained from the nearest available US Geological Survey gaging station (<http://waterdata.usgs.gov/nwis/rt>). Correlation between putative annual growth increments and a strong, variable environmental signal (e.g. annual streamflow) can provide convincing support for the annual formation of increments (Black, Boehlert & Yoklavich, 2005) and a negative relationship between mean annual flow and mussel growth has been shown previously (Rypel *et al.*, 2008; Rypel, Haag & Findlay, 2009; Black *et al.*, in press). Mussel growth is related similarly to other hydrologic variables (e.g. negatively correlated with spring flows and flood pulse count; Rypel *et al.*, 2009), but because these variables are correlated positively with mean annual discharge, we used annual flow as the simplest and most inclusive measure of annual variation in flow. Applicable gaging stations were not available for five populations and in these cases we used interseries correlations only for validation purposes.

(5) Data analysis

We characterized freshwater mussel growth with the von Bertalanffy growth equation

$$L_t = L_{\text{inf}}(1 - e^{-K(t-t_0)}) \quad (1)$$

where L_t is length (mm) at time t (age in years), L_{inf} is length (mm) at time infinity (the predicted mean maximum length for the population), K is a growth constant that describes the

rate at which L_{inf} is attained (mm year^{-1}), t is age (years) and t_0 is the time at which length = 0 (Ricker, 1975). We estimated von Bertalanffy parameters separately for each population using nonlinear least-squares regression (SAS, 2002–2003) based on mean length at age. We estimated growth parameters separately for males and females in species that could be sexed reliably based on shell characters, or for live-collected specimens whose sex could be determined by examining gonadal material (see Haag & Staton, 2003).

We tested for differences in growth parameters between sexes and between conspecific populations using likelihood ratio tests (Kimura, 1980). In this procedure, we calculated a coincident von Bertalanffy equation by combining all individuals from both sexes or all populations being compared. We then compared residual sum of squares for coincident equations and each parameter against the total sums of squares for the base case equation which represented the additive sums of squares for each sex or population. Growth equations or parameters were considered different between sexes or populations if the base case produced a significantly better fit than coincident equations relative to the chi-squared distribution (Kimura, 1980). We did not report test results for the parameter t_0 because this parameter has little biological meaning (Ricker, 1975).

We examined relationships among growth variables across 126 populations (52 species) in our data set that had complete growth data; we had shell mass data for only 69 populations. We considered males and females as separate populations for species in which sexes had significantly different growth parameters. First, we examined bivariate relationships among growth rate (K), longevity (A_{max}), maximum size (L_{max}), and relative shell mass (RM). All variables were \log_{10} transformed to achieve homogeneity of variances except RM which is a ratio of log-transformed variables (see Section II.2). Second, because body size is correlated strongly with many life-history traits and may obscure relationships with other variables (Calder, 1984; Bonsall, 2005), we were interested in examining patterns of longevity and growth with the effect of size removed. We obtained length-standardized values for K and A_{max} by regressing these variables (log transformed) on $\log L_{\text{max}}$ and using the residuals of these regressions in subsequent comparisons (e.g. White & Seymour, 2004). Third, to account for potential phylogenetic effects on relationships between variables, we computed phylogenetically independent contrasts (Felsenstein, 1985) for the log-transformed values of K , A_{max} , and L_{max} using PHYLIP (Felsenstein, 2005). This procedure results in $N-1$ contrasts that are phylogenetically independent. Because these contrasts have a mean expectation of zero, relationships between phylogenetically independent contrasts were analyzed by regressing these variables through the origin (Garland, Harvey & Ives, 1992). Our phylogeny was based on genetic distance data for the mitochondrial gene regions COI and ND1 from Campbell *et al.* (2005) and D. Campbell (unpublished data). We did not compute phylogenetically independent contrasts for RM because shell mass data were not available for all species in the phylogenetic data set.

Table 2. Cross-dating statistics for 42 populations of freshwater mussels. All interseries correlations (Pearson's) were significant at $P < 0.05$. Significant correlations of growth with mean annual streamflow (Pearson's r) are denoted as $*P < 0.05$ and $**P < 0.01$. US Geological Survey (USGS) gaging stations used as sources for streamflow data are identified as per <http://waterdata.usgs.gov/nwis/rt>. †, streamflow data were not available for Shoal Creek, AL; these correlations are based on data from a nearby stream (Choccolocco Creek). –, no correlations are available for sites without streamflow data or data for similar, nearby streams

Species	Site	Time series	Mean interseries r	Correlation with streamflow	USGS streamflow gage
<i>Alasmidonta viridis</i>	Brushy Creek, KY	1987–2003	0.63	–	–
<i>Elliptio arca</i>	Buttahatchee River, MS	1973–1999	0.60	–0.74**	02438000
<i>Elliptio crassidens</i>	Buttahatchee River, MS	1952–1992	0.60	–0.40**	02438000
<i>Epioblasma penita</i>	Buttahatchee River, MS	1992–1999	0.64	–0.05	02438000
<i>Fusconaia cerina</i>	Buttahatchee River, MS	1986–1998	0.53	–0.62*	02438000
<i>Quadrula asperata</i>	Buttahatchee River, MS	1981–1999	0.52	–0.66**	02438000
<i>Toxolasma parva</i>	Davis Lake, MS	1995–1998	0.81	–	–
<i>Pyganodon grandis</i>	Kettle Creek, MS	1992–1999	0.54	–	–
<i>Toxolasma texasensis</i>	Kettle Creek, MS	1990–1999	0.49	–	–
<i>Villosa lienosa</i>	Kettle Creek, MS	2000–2005	0.75	–	–
<i>Plectomerus dombeyanus</i>	Leaf River, MS	1991–2004	0.73	0.42	02473000
<i>Alasmidonta marginata</i>	Licking River, KY	1984–1992	0.74	–0.52	03251500
<i>Cyprogenia stegaria</i>	Licking River, KY	1976–1993	0.77	–0.53*	03251500
<i>Lasmigona costata</i>	Licking River, KY	1987–2007	0.92	–0.47**	03251500
<i>Leptodea fragilis</i>	Licking River, KY	1986–1992	0.97	–0.04	03251500
<i>Obliquaria reflexa</i>	Licking River, KY	1980–1992	0.78	–0.48	03251500
<i>Pleurobema coccineum</i>	Licking River, KY	1970–1998	0.65	–0.40*	03251500
<i>Ptychobranchus fasciolaris</i>	Licking River, KY	1980–2008	0.68	–0.90**	03251500
<i>Quadrula pustulosa</i>	Licking River, KY	1977–1992	0.79	–0.53*	03251500
<i>Truncilla donaciformis</i>	Licking River, KY	1986–1992	0.48	–0.75*	03251500
<i>Truncilla truncata</i>	Licking River, KY	1984–1992	0.25	–0.45	03251500
<i>Plectomerus dombeyanus</i>	Pearl River, MS	1970–2004	0.45	–0.16	02482550
<i>Potamilus purpuratus</i>	Pearl River, MS	1982–2005	0.16	0.13	02482550
<i>Pyganodon grandis</i>	Pearl River, MS	1997–2005	0.53	–0.27	02482550
<i>Quadrula refulgens</i>	Pearl River, MS	1975–2005	0.46	0.41*	02482550
<i>Hamiota altilis</i>	Shoal Creek, AL	1990–2002	0.51	–0.59*	02404400†
<i>Strophitus subvexus</i>	Shoal Creek, AL	1986–2002	0.72	–0.01	02404400†
<i>Villosa nebulosa</i>	Shoal Creek, AL	1992–2002	0.42	–0.71*	02404400†
<i>Villosa vibex</i>	Shoal Creek, AL	1994–2002	0.53	–0.40	02404400†
<i>Amblema plicata</i>	Sipsey River, AL	1953–1999	0.46	–0.42**	02446500
<i>Lampsilis straminea</i>	Sipsey River, AL	1988–2005	0.55	–0.58**	02446500
<i>Lampsilis teres</i>	Sipsey River, AL	1996–2005	0.82	–0.60*	02446500
<i>Medionidus acutissimus</i>	Sipsey River, AL	1998–2006	0.99	–0.90	02446500
<i>Megalonaias nervosa</i>	Sipsey River, AL	1971–2005	0.78	–0.50**	02446500
<i>Obovaria jacksoniana</i>	Sipsey River, AL	1992–2005	0.65	–0.36	02446500
<i>Villosa lienosa</i>	Sipsey River, AL	2000–2005	0.78	–0.94*	02446500
<i>Cyprogenia aberti</i>	Spring River, AR	1982–1994	0.64	–0.14	7069500
<i>Ligumia recta</i>	St. Croix River, MN	1988–2001	0.72	–0.59*	05340500
<i>Truncilla truncata</i>	St. Croix River, MN	1997–2007	0.65	–0.64**	05340500
<i>Ellipsaria lineolata</i>	Tennessee River, AL	1983–2000	0.52	–0.24	03589500
<i>Ligumia recta</i>	Tennessee River, AL	1993–2000	0.88	–0.26	03589500
<i>Quadrula asperata</i>	Tombigbee River, MS	1991–2004	0.27	–0.57*	02433500

Lastly, we used path analysis to evaluate the relative contributions of growth rate, size, and shell mass in explaining observed variation in longevity. Path analysis is an extension of multiple regression that allows construction of causal paths between multiple independent and dependent variables and provides a means of decomposing correlations between variables into causal and noncausal contributions (Schemske & Horvitz, 1988). For this analysis, we used data that were not

corrected for phylogenetic effects because phylogenetically independent contrasts for shell mass were not available.

We developed the path structure we consider most appropriate for describing the relationship among growth variables of freshwater mussels based on observed bivariate relationships among these variables (see Section III). We estimated path coefficients between variables as the standardized partial regression coefficients of independent variables in multiple

or single-factor regressions. We decomposed correlations between variables into direct and indirect effects following Schemske & Horvitz (1988) and Sokal & Rohlf (1995).

III. RESULTS

Annual growth rings were uninterpretable for only one species, *Unio merus tetralasmus*, from a population in Mississippi. Thin sections of this species had a large number of rings of variable appearance that were uninterpretable with criteria used to identify annual rings in other species. Thin sections of all other species were readily interpretable and had over 90% agreement between interpretations of independent observers. Growth was described well by von Bertalanffy equations for all species. Across all species, asymptotic length (L_{inf}) was a good predictor of observed maximum size ($F = 6952.34$, $P < 0.0001$, $r^2 = 0.970$; \log_{10} -transformed data) and the slope and intercept of this relationship did not differ significantly from 1 and 0, respectively ($\log_{10}L_{\text{max}} = 1.0076(\log_{10}L_{\text{inf}}) + 0.0127$).

(1) Validation of annual rings

Cross-dating supported the assumption of annual ring formation and the accuracy of our interpretations in the 42 populations that had not been validated previously (Table 2). Out of 447 total specimens cross-dated from these populations, quality control identified 62 potential errors. We identified and corrected errors in 25 of these specimens and excluded two specimens from the data set due to disagreement between observers; all others were left unchanged. After quality control, all interseries correlations were significant and ranged from 0.16 to 0.99 (mean = 0.61); these values are similar to or higher than validated growth patterns for other organisms (see Rypel *et al.*, 2008) and indicate that growth is highly synchronous among individuals within most of these populations.

Growth was negatively and significantly correlated with mean annual streamflow in 20 out of 37 populations with flow data, providing strong evidence that the shell rings we interpreted reflect annual growth patterns. In 14 other populations, signs of the correlation coefficients were negative but the relationship was not significant (Table 2). Some of these non-significant correlations are probably due to the short chronologies of short-lived species (e.g. *Alasmidonta marginata*, *Leptodea fragilis*, *Strophitus subvexus*, *Villosa vibex*) which resulted in low power to detect a relationship with flow; however, in six of these populations [*Alasmidonta marginata*, *Obliquaria reflexa*, *Obovaria jacksoniana*, *Strophitus subvexus*, *Truncilla truncata* (Licking River), *Villosa vibex*] growth was significantly and positively correlated with other species at the same site that had significant, negative correlations with flow. Growth was correlated positively with flow in three populations, but was significant only for *Quadrula refulgens* from an impounded site on the Pearl River. No other populations in impounded streams (Tennessee and

Pearl Rivers) had significant correlations of growth and flow. Because impoundment can disrupt relationships with flow (Rypel *et al.*, 2008), we considered annual rings validated in these populations based on their significant interseries correlations (Table 2). Only one population from a free-flowing stream had a positive, but non-significant correlation between growth and flow (*Plectomerus dombeyanus*, Leaf River), but this population had a high interseries correlation ($r = 0.73$) indicating high growth synchrony in this population.

(2) Age and growth variation among species and phylogenetic groups

Growth and longevity varied greatly across species (see Table 1). In our original data set, values of the growth constant K ranged from 0.05 (*Quadrula asperata*, slow-growing form, see below) to 1.01 (*Toxolasma parva*) and maximum age ranged from 4–5 years (*Leptodea fragilis*, *Medionidus acutissimus*, *T. parva*) to 72 years (*Q. asperata*, slow-growing form). Other long-lived species included *Elliptio crassidus* (57 years), *Amblema plicata* (54 years), *Quadrula pustulosa* (48 years), *Fusconaia cerina*, and *Pleurobema decisum* (both 45 years). Values of K reported in the literature ranged from 0.02 (*Margaritifera margaritifera*) to 0.41 (*Unio terminalis*) and longevity ranged from 9–10 years (*Alasmidonta heterodon*, *Anodonta piscinalis*, *Toxolasma pullus*, and *U. terminalis*) to 190 years (*M. margaritifera*). Other species reported in the literature to reach advanced ages included *Margaritifera falcata* (100 years), *Cyclonaias tuberculata* (91 years), *Cumberlandia monodonta* (56 years), *Fusconaia ebena* (51 years), and *Actinonaias ligamentina* (~50 years).

Longevity varied among major taxonomic groups of mussels but most groups showed considerable variability (Fig. 1). Short-lived species with longevity <14 years were restricted to the tribes Anodontini and Lampsilini. Anodontini and Lampsilini had similar median longevity but Anodontini were consistently short-lived (range = 7–19 years) whereas Lampsilini had a much wider range of longevity (4–50 years). The other mussel groups were longer-lived. The tribes Amblemini, Pleurobemini, and Quadrulini had a wide range of longevities (Amblemini, 18–54 years; Pleurobemini, 14–57; Quadrulini, 15–91) but median longevity of these tribes was about twice that of Anodontini or Lampsilini (Fig. 1). The family Margaritiferidae had the highest median maximum age but longevity ranged from 28 to 190 years.

Values of the growth rate K also differed among taxonomic groups but showed an opposite pattern than longevity. Median values of K were highest for Anodontini and Lampsilini and were similar for these two tribes, but both showed high variation in K (Fig. 1). However, no species of Anodontini had $K < 0.20$, but Lampsilini had both the highest value of K of any group (1.01) as well low values (0.08) that were similar to long-lived tribes. The Amblemini, Pleurobemini, Quadrulini, and Margaritiferidae all had low median values of K and showed much less variation in this trait than Anodontini and Lampsilini (Fig. 1).

In contrast to longevity and growth rate, maximum size (L_{max}) and relative shell mass (RM) showed little consistent variation among groups (Fig. 1). Small species (<50 mm)

were restricted to the tribes Anodontini and Lampsilini but the range of maximum size overlapped widely for all groups and median maximum size showed no clear pattern. Variation in relative shell mass among groups showed some similarity to variation in longevity. Tribes with low median longevity (Anodontini and Lampsilini) had lower median relative shell mass than the longer lived tribes Amblemini, Pleurobemini, and Quadrulini. However, the group with the greatest median longevity, the Margaritiferidae, had low relative shell mass that was similar to the short-lived Anodontini. Furthermore, the Lampsilini had a very wide range of relative shell mass including both the lowest (*Medionidus acutissimus*) and highest (*Potamilus purpuratus*) observed values in our data set.

(3) Variation among populations

Age and growth differed among many populations. In our data set, growth was significantly different between conspecific populations in different rivers in nine of 13 comparisons. In nearly all of these nine comparisons, differences between base case and coincident equations and all von Bertalanffy parameters were highly significant (Table 3); the only exceptions were *Lampsilis teres* and *Quadrula asperata*, for which the difference in K was only marginally significant even though L_{inf} and maximum size differed greatly (Fig. 2). Longevity often differed substantially between populations both in our original data and in literature reports. For example, maximum age of *Amblema plicata* in the Sipsey River was 54 years but the oldest individual in the Little Tallahatchie River was

Table 3. Comparisons of growth variables between mussel populations. River codes are as follows: BH, Buttahatchee; KC, Kettle Creek; LK, Licking; LT, Little Tallahatchie; LF, Leaf; PR, Pearl; SP, Sipsey; SC, St. Croix; SF, St. Francis; TN, Tennessee; TB, Tombigbee. Growth equation parameters and site locations are given in Table 1. SSQ = sum of squares; see Section II.5 for description of base case and coincident equations. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For marginally significant statistics ($P < 0.1$), P values appear in superscript; all other values are non-significant. Comparisons involving *Quadrula asperata* from the Sipsey River exclude a distinctive, slow-growing form found in the river (see Section III.4.b and Fig. 4)

Species (populations)	Statistic	Base case equation	Coincident equation	L_{inf}	K
<u>Comparisons among rivers</u>					
<i>Amblema plicata</i> (SP–LT)	SSQ	684.47	6885.75	1145.43	2415.62
	χ^2		84.22***	18.78***	46.01***
<i>Elliptio arca</i> (SP–BH)	SSQ	860.97	896.35	865.37	861.62
	χ^2		2.20	0.28	0.04
<i>Fusconaia cerina</i> (SP–BH)	SSQ	542.76	698.76	548.45	556.83
	χ^2		2.63	0.48	1.18
<i>Ligumia recta</i> (SC–TN)	SSQ	600.48	6529.17	1465.54	1238.03
	χ^2		37.31***	13.95***	11.31***
<i>Lampsilis teres</i> (SP–SF)	SSQ	1553.50	6834.53	2362.07	1750.17
	χ^2		41.18***	11.65***	3.31 ^{<0.07}
<i>Obliquaria reflexa</i> (SP–LK)	SSQ	266.37	757.84	356.89	340.18
	χ^2		29.97***	8.39**	7.01**
<i>Plectomerus dombeyanus</i> (PR–LF)	SSQ	1125.70	1494.34	1344.84	1384.02
	χ^2		8.37*	5.25*	6.10*
<i>Potamilus purpuratus</i> (PR–SF, males)	SSQ	2974.20	3399.64	3159.13	3382.77
	χ^2		2.55	1.15	2.46
<i>Quadrula asperata</i> (SP–BH)	SSQ	725.56	823.49	733.90	728.18
	χ^2		2.69	0.78	0.25
<i>Q. asperata</i> (SP + BH – TB)	SSQ	852.60	4244.09	1994.33	894.96
	χ^2		121.28***	64.22***	3.66 ^{<0.06}
<i>Q. pustulosa</i> (LK–LT)	SSQ	452.14	1513.96	607.02	745.16
	χ^2		49.33***	12.03***	20.40***
<i>Truncilla truncata</i> (SC–LK)	SSQ	118.66	1319.60	310.40	178.91
	χ^2		41.85***	16.70***	7.13**
<i>Villosa lienosa</i> (SP–KC)	SSQ	58.75	259.32	145.93	143.69
	χ^2		19.34***	11.85***	11.65***
<u>Comparisons within rivers</u>					
<i>E. arca</i> (SP, three populations)	SSQ	783.78	1187.70	801.67	832.47
	χ^2		6.58 ^{<0.09}	1.12	2.98 ^{<0.08}
<i>Q. asperata</i> (SP, three populations)	SSQ	579.51	721.49	603.30	624.44
	χ^2		7.27 ^{<0.07}	3.35	5.23 ^{<0.07}

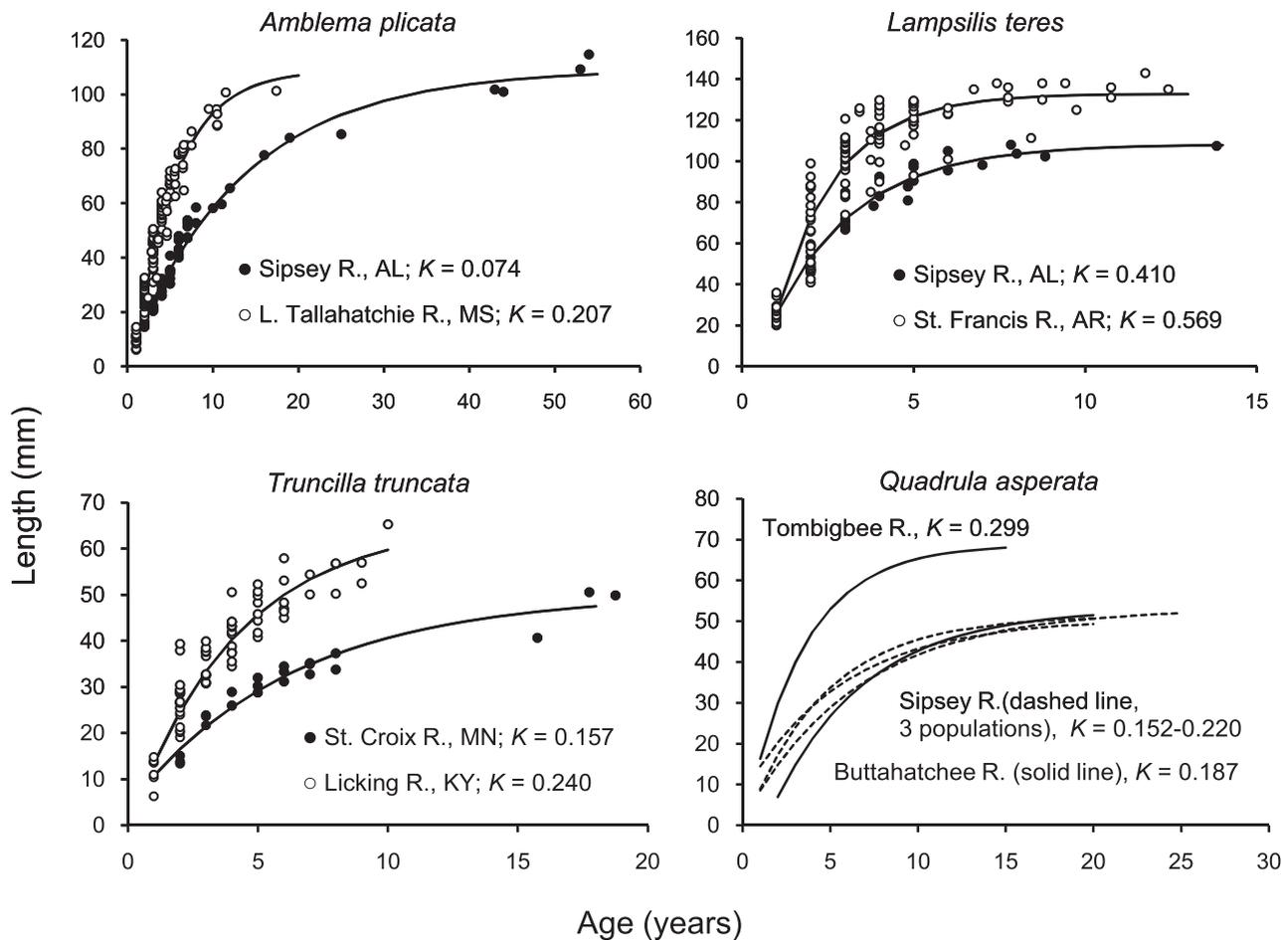


Fig. 2. von Bertalanffy growth curves showing among-population differences in growth of freshwater mussels. Parameters for growth equations for all curves are given in Table 1. For clarity, observed points are not shown on the graph for *Quadrula asperata* due to the large number of populations with similar curves; this graph omits a distinctive, slow-growing form of *Q. asperata* found in the Sipsey River (see Section III.4.b and Fig. 4).

only 18 years (Fig. 2). Similarly, longevity varied from 28 to 190 years among populations of *Margaritifera margaritifera*, representing greater than a sixfold difference (Table 1). In all cases, populations that had significantly lower values of K had higher maximum ages (Fig. 2, Table 1). The only populations between which growth did not differ were those in the Sipsey and Buttahatchee Rivers (three species, Fig. 2, Table 3) and between populations of *Potamilus purpuratus* in the Pearl and St. Francis Rivers (Table 3). For two species, *Elliptio arca* and *Quadrula asperata*, growth was similar among three populations in the Sipsey River. Differences in base case and coincident equations and K were marginally significant for both species (Table 3) but L_{inf} did not differ and overall growth trajectories were similar (Fig. 2).

(4) Variation within populations

(a) Sex differences

Growth differed between sexes for some species but not for others. In general, growth did not differ between sexes

in species that do not exhibit strong sexual dimorphism in shell shape. Growth of male and female *Quadrula asperata* and *Q. refulgens* was indistinguishable (Table 4). For *Elliptio arca*, *Pleurobema decisum*, and *Quadrula rumphiana*, base case and coincident growth equations were significantly different, but few or no von Bertalanffy parameters differed between males and females (Table 4) and growth trajectories overall were similar between sexes (Fig. 3). *Obliquaria reflexa* was the only species without strong shell sexual dimorphism in which sexes had a significantly different growth trajectory. For this species, the growth constant K was significantly lower in females (Table 4) but females ultimately attained a similar size as males (Fig. 3). Maximum age was similar between sexes for all of these species.

Growth differed between sexes for most species that exhibit strong shell sexual dimorphism. Seven of ten sexually dimorphic species had significant differences between sexes in base case and coincident growth equations and most von Bertalanffy parameters (Table 4). Differences in the growth constant K showed no clear pattern among sexes; K was

Table 4. Comparisons of growth variables between sexes for freshwater mussels. All populations are from the Sipsey River unless indicated otherwise. Codes for other rivers are as follows: BH, Buttahatchee; KC, Kettle Creek; PR, Pearl; SH, Shoal Creek, SF, St. Francis. Growth equation parameters and site locations are given in Table 1. SSQ = sum of squares; see Section II.5 for description of base case and coincident equations. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For marginally significant statistics ($P < 0.1$), P -values appear in superscript; all other values are non-significant. Comparisons involving *Quadrula asperata* from the Sipsey River exclude a distinctive, slow-growing form found in the river (see Section III.4.b and Figure 4)

Species (population)	Statistic	Base case equation	Coincident equation	L_{inf}	K
<i>Elliptio arca</i>	SSQ	1406.74	2569.27	1596.61	1617.83
	χ^2		12.56**	2.64	2.91 ^{<0.09}
<i>Lampsilis straminea</i>	SSQ	311.48	370.95	369.65	353.92
	χ^2		3.34	3.27 ^{<0.07}	2.44
<i>Medionidus acutissimus</i>	SSQ	26.07	32.16	29.15	28.47
	χ^2		2.01	1.07	0.84
<i>Obovaria jacksoniana</i>	SSQ	131.66	289.45	148.33	151.93
	χ^2		19.16***	2.90 ^{<0.09}	3.48*
<i>O. unicolor</i>	SSQ	158.02	381.64	200.06	164.55
	χ^2		32.93***	8.81**	1.51
<i>Obliquaria reflexa</i>	SSQ	245.14	373.77	249.05	279.02
	χ^2		13.56**	0.51	4.16*
<i>Pleurobema decisum</i>	SSQ	133.89	204.57	134.55	136.64
	χ^2		9.94**	0.12	0.48
<i>Potamilus purpuratus</i> (SF)	SSQ	1370.56	5680.24	2167.01	1559.96
	χ^2		28.40***	9.15**	2.59
<i>Quadrula asperata</i>	SSQ	67.40	84.82	75.49	74.24
	χ^2		3.59	1.77	1.51
<i>Q. asperata</i> (BH)	SSQ	327.23	359.80	333.38	335.99
	χ^2		1.90	0.37	0.53
<i>Q. refulgens</i> (PR)	SSQ	85.00	89.53	88.79	86.53
	χ^2		1.27	1.06	0.43
<i>Q. numphiana</i>	SSQ	304.00	383.48	327.92	304.02
	χ^2		8.07*	2.63	0.00
<i>Toxolasma texasense</i> (KC)	SSQ	8.67	325.98	59.83	16.78
	χ^2		44.10***	23.49***	8.03**
<i>Q. verrucosa</i>	SSQ	434.33	843.36	727.21	551.35
	χ^2		21.90***	17.01***	7.87**
<i>Villosa lienosa</i> (KC)	SSQ	69.80	96.58	74.40	71.50
	χ^2		3.10	0.61	0.23
<i>V. nebulosa</i> (SH)	SSQ	18.23	34.49	28.02	27.77
	χ^2		8.31*	5.60*	5.48*
<i>V. vibex</i> (SH)	SSQ	20.45	76.65	1899.79	124.04
	χ^2		17.21***	59.04***	23.48***

higher for females in three species, lower in two, and not significantly different in two species. For all but one sexually dimorphic species, males reached considerably larger sizes than females (Fig. 3, Table 1). The only exception to this pattern was *Quadrula verrucosa* in which females were larger than males (Fig. 3). In general, females had lower maximum ages than males (Table 1) but maximum age was similar between sexes of *Potamilus purpuratus* and *Toxolasma texasense*; however, sample sizes were too small for most species to evaluate differences in longevity between sexes. Growth trajectories did not differ between sexes of *Lampsilis straminea*, *Medionidus acutissimus*, and *Villosa lienosa* (Table 4) even though

sexes of these species are readily distinguishable based on the marsupial expansion of female shells.

(b) Other within-population patterns

A population of *Quadrula asperata* in the Sipsey River exhibited two distinctly different growth trajectories (Fig. 4). Most individuals in this population grew similarly to other populations of *Q. asperata* and to other *Quadrula* species, having a low-to-moderate value of K (0.152) and intermediate maximum age (27 years). By contrast, a subset of this population (10 individuals) showed extremely slow growth ($K = 0.05$) and

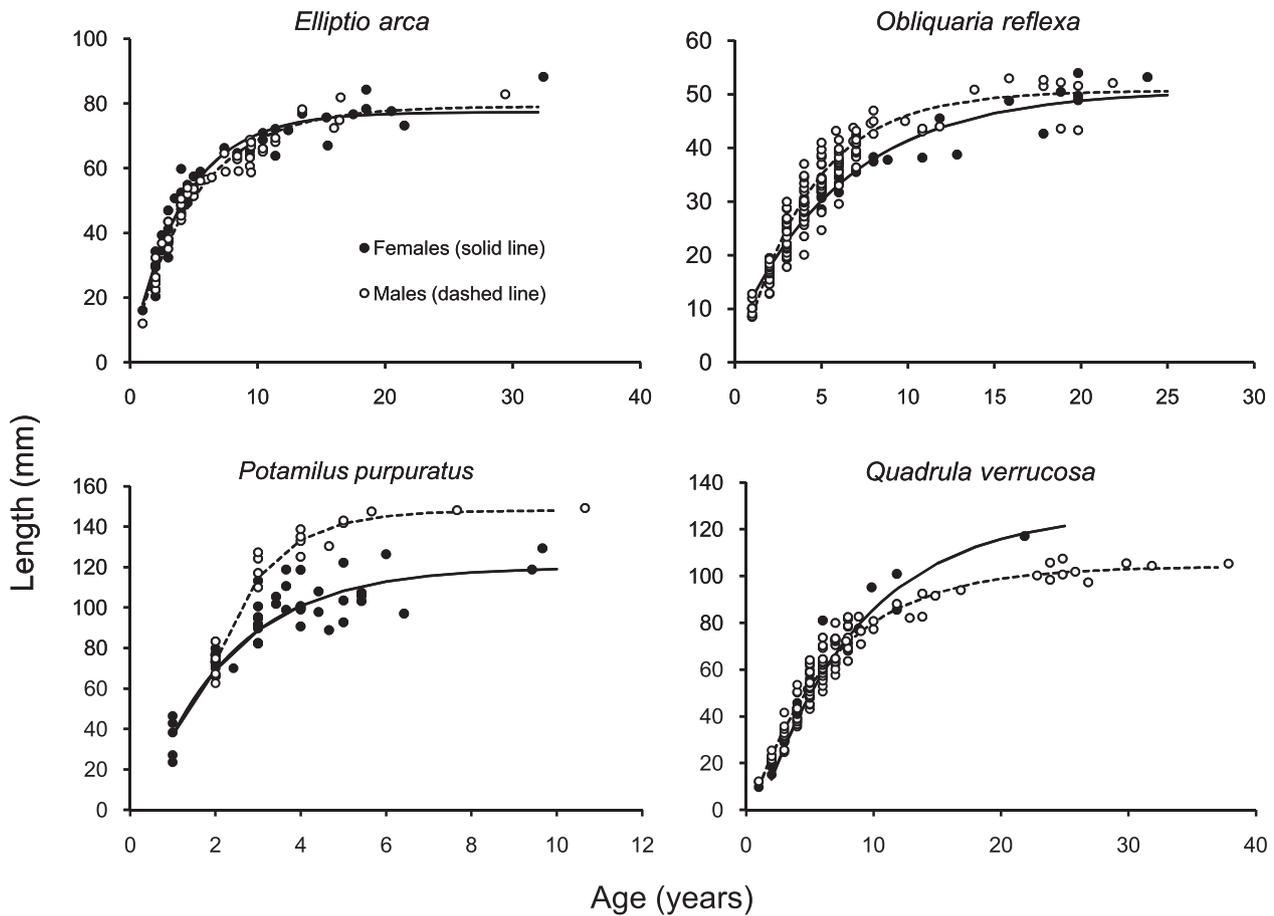


Fig. 3. von Bertalanffy growth curves showing sex-specific patterns of growth of freshwater mussels. Parameters for growth equations for all curves are given in Table 1.

reached advanced ages (maximum age = 72 years). Slow-growing individuals were easily recognized, being diminutive and having tightly crowded annual rings; after age three years, mean length at age was about 60% of other individuals in the population (Fig. 4). Base case and coincident growth equations and all von Bertalanffy parameters were significantly different between slow-growing individuals and the remainder of the population [coincident equation: sum of squares (SSQ) = 1671.51, $\chi^2 = 61.35$, $P < 0.0001$; L_{inf} : SSQ = 425.49, $\chi^2 = 9.06$, $P = 0.002$; K : SSQ = 534.64, $\chi^2 = 17.79$, $P < 0.0001$]. We were not able to determine the sex of slow-growing individuals. No other populations in our data set, even those with large sample sizes, exhibited this type of within-population divergence in growth trajectories.

(5) Relationships among growth variables

Across all species and populations, longevity (A_{max}) was strongly negatively related to the growth rate, K , in the form of a power function, and K explained $>75\%$ of the variation in longevity (Fig. 5). By contrast, A_{max} was positively related to maximum size (L_{max}) and relative shell mass (RM) but these relationships explained little of the variation in age; many

smaller species (<80 mm) reached advanced ages (>40 years) and many large species were short-lived (Fig. 5). When the effect of size on A_{max} was removed, there remained a strong, negative relationship between longevity and K (Fig. 5). All other growth variables were intercorrelated. There was a negative but weak relationship between L_{max} and K and between RM and K (Fig. 6). Relative shell mass was positively related to L_{max} and this relationship explained a moderate amount of the variation in RM (Fig. 6).

When the effect of phylogeny was removed, the percentage of variation explained in bivariate relationships between growth variables decreased by about 20–40% (Fig. 7). This result shows that inherited differences among lineages explain a significant portion of the variation in growth rate, longevity, and size observed among species. However, the overall pattern of all relationships remained and K continued to be the strongest predictor of longevity (Fig. 7). Furthermore, within phylogenetic lineages there was a strong relationship between K and longevity. For example, K explained 79% of the variation (r^2) in longevity within the lampsiline clade consisting of *Cyprogenia*, *Dromus*, *Medionidus*, *Ptychobranchus*, *Leptodea*, and *Potamilus* (12 populations, see Campbell *et al.*, 2005), and 86% of variation in the *Quadrula pustulosa* group

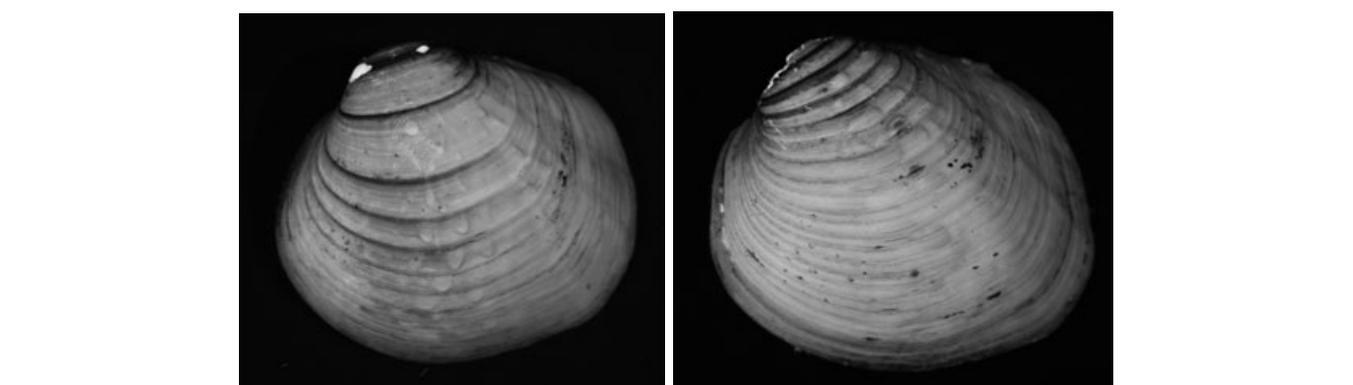
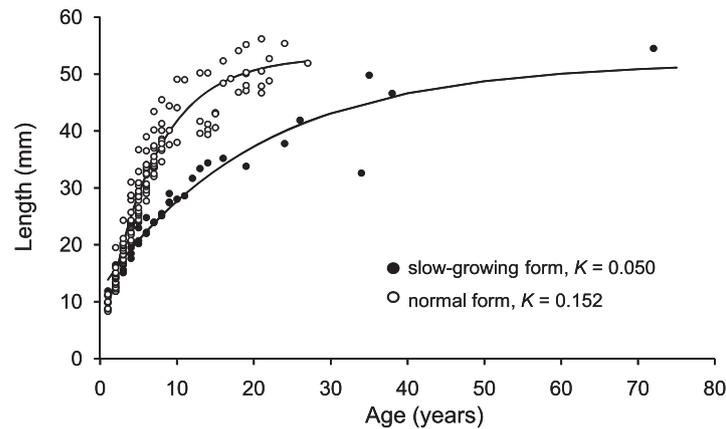


Fig. 4. von Bertalanffy growth curves (top panel) showing differences in growth and longevity between two subsets of a population of *Quadrula asperata* in the Sipsy River, AL. Parameters for growth equations for both curves are given in Table 1. The lower panel shows the external shell morphology of normal (left; length = 47.5 mm, age = 16 years) and slow-growing (right; 50.9 mm, 35 years) forms of *Q. asperata*. Note widely spaced growth rings in normal form *versus* closely spaced rings in slow-growing form.

(tribe Quadrulini, nine populations, including in our data set *Q. asperata*, *Q. pustulosa*, and *Q. refulgens*; see Serb, Buhay & Lydeard, 2003).

Path analysis identified the growth rate, K , as the strongest predictor of longevity (Fig. 8). Together, K , L_{\max} , and relative shell mass (RM) explained nearly 80% of the variation in longevity but the effect coefficient for K was four times higher than the coefficients of the other two variables (Table 5). Growth rate had a negative effect on longevity and was manifested predominantly as a direct effect. Relative shell mass had a small, positive effect on longevity and, in addition, both K and L_{\max} had small, indirect effects on longevity through their effects on relative shell mass (Fig. 8). Growth rate and L_{\max} explained >60% of the variation in RM (Table 5). Length had a positive effect on RM but K had a negative effect and acted on RM both directly and indirectly through its effect on L_{\max} . Even though the indirect effect of K on RM (via the effect of K on L_{\max}) was of moderate magnitude (-0.397), the direct effect of K on L_{\max} was not significant (Table 5), suggesting that this pathway is of little predictive importance. The direct effect of L_{\max} on longevity was of small magnitude and was not significant, suggesting that the bivariate relationship between L_{\max} and longevity (Fig. 5) is spurious and is an artifact of the effect of L_{\max} on RM .

IV. DISCUSSION

(1) Growth variation at multiple levels

Apparent differences in age and growth among major phylogenetic groups of mussels have been noted for many years (e.g. Coker *et al.*, 1921; Stansbery, 1967). However, these generalizations are of only limited use because of the variation present within most groups. Our data support previous categorizations of short life span and fast growth for the Anodontini and conversely, long life and slow growth in the Margaritiferidae. However, even though the tribes Amblemini, Pleurobemini, and Quadrulini may be categorized as long-lived and slow-growing based on their median values of longevity and growth that are similar to the Margaritiferidae, the range of values seen in these groups also overlaps with the Anodontini and Lampsilini. The tribe Lampsilini is usually characterized as short-lived and fast-growing or “intermediate” in these traits (e.g. Stansbery, 1967) but values of longevity and growth rate within the group overlap widely with all other groups including short-lived Anodontini and long-lived Margaritiferidae.

Even within species, generalizations about longevity and growth must consider the variation present among

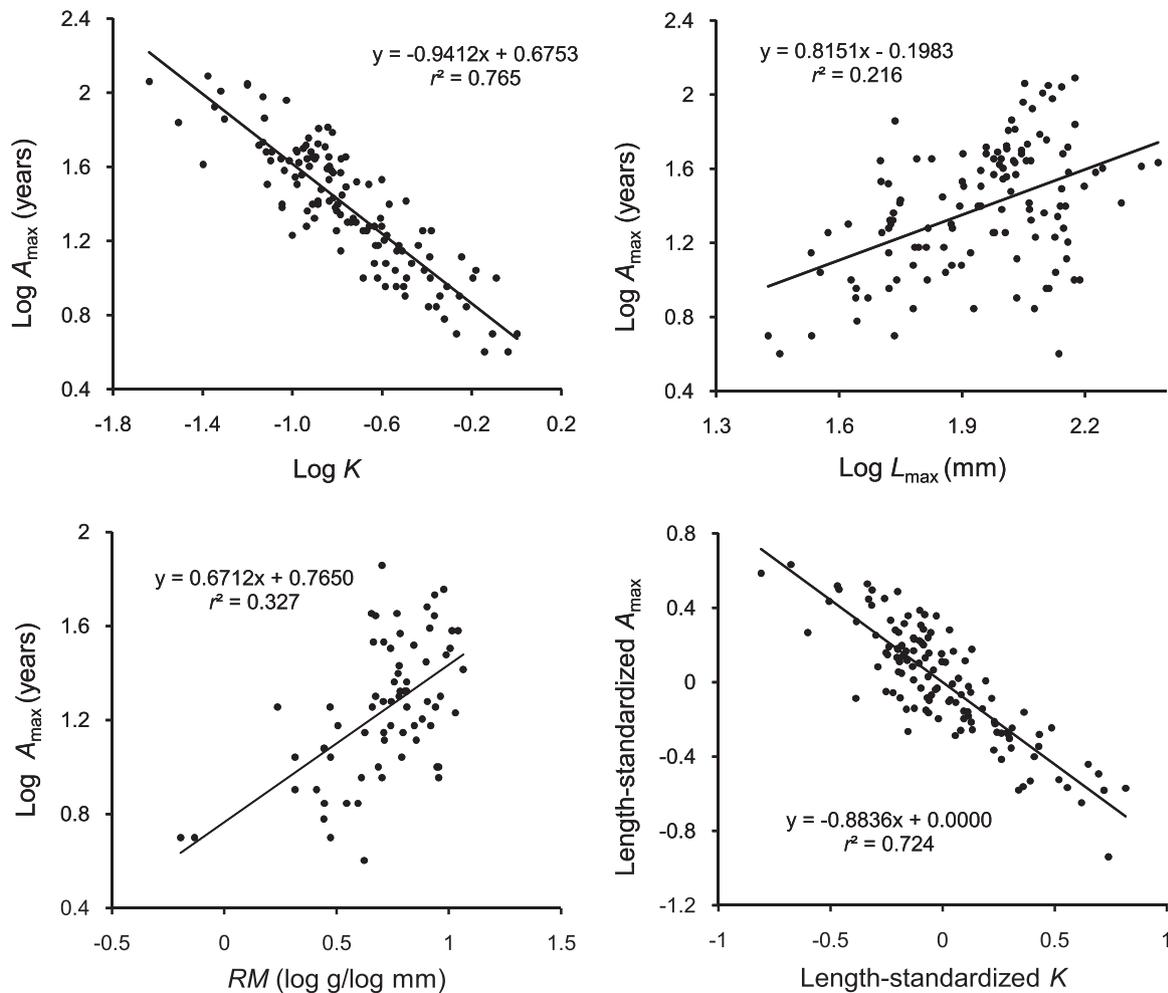


Fig. 5. Relationships between longevity (A_{\max}) and growth variables of freshwater mussels. K is the von Bertalanffy growth constant, L_{\max} is maximum observed length, and RM is relative shell mass expressed as log mass/log length (g mm^{-1}). Length-standardized variables (lower right panel) are residuals of \log_{10} -transformed values regressed on \log_{10} length. All regressions are significant at $P < 0.0001$.

populations. Longevity and growth differed between many conspecific populations by a factor of 2–6. In several species, more northerly populations had lower growth rates but greater longevity (e.g. *Leptodea fragilis*, *Ligumia recta*, *Truncilla truncata*; see Table 1). Similar latitudinal patterns have been reported previously in freshwater mussels (*Margaritifera margaritifera* and *Unio crassus*; Bauer, 1992; Hochwald, 2001; Helama & Valovirta, 2008) as well as marine bivalves (e.g. Bachelet, 1980; Nichols & Thompson, 1982), and are attributed to lower water temperatures and shorter growing seasons in northern latitudes (Dunca & Mutvei, 2001; Schöne *et al.*, 2004). In other cases, differences in growth between populations may be related to differences in water chemistry between river basins. Calcium and bicarbonate concentrations are important for mollusc shell production and decreases in levels of these ions can result in thinner and smaller shells (Nduku & Harrison, 1976; Mackie & Flippance, 1983; Hinch, Kelly & Green, 1989). In our study, growth rate and maximum size of several species in the

Sipsey and Buttahatchee Rivers in AL and MS was lower than in other populations at similar latitudes (*Amblema plicata*, Little Tallahatchie River, MS; *Quadrula asperata*, Tombigbee River, MS) or more northerly populations (*Obliquaria reflexa*, Licking River, KY). The Sipsey and Buttahatchee Rivers flow through a region underlain by Cretaceous sands and clays and have low bicarbonate concentrations ($7\text{--}13\text{ mg l}^{-1}$) relative to these other streams ($52\text{--}100\text{ mg l}^{-1}$, data from US Geological Survey, <http://waterdata.usgs.gov/nwis/qw>). Other water chemistry and physical factors are likely to influence mussel growth. Mussel populations in enriched rivers or lakes grow more rapidly than populations in less productive waters (Morris & Corkum, 1999; Valdovinos & Pedreros, 2007), and sediment type, variation in streamflow, exposure to wind and current, and perhaps food limitation can also influence growth rate and shell size (Hinch, Bailey & Green, 1986; Bailey & Green, 1988; Griffiths & Cyr, 2006; Kesler, Newton & Green, 2007; Rypel *et al.*, 2009).

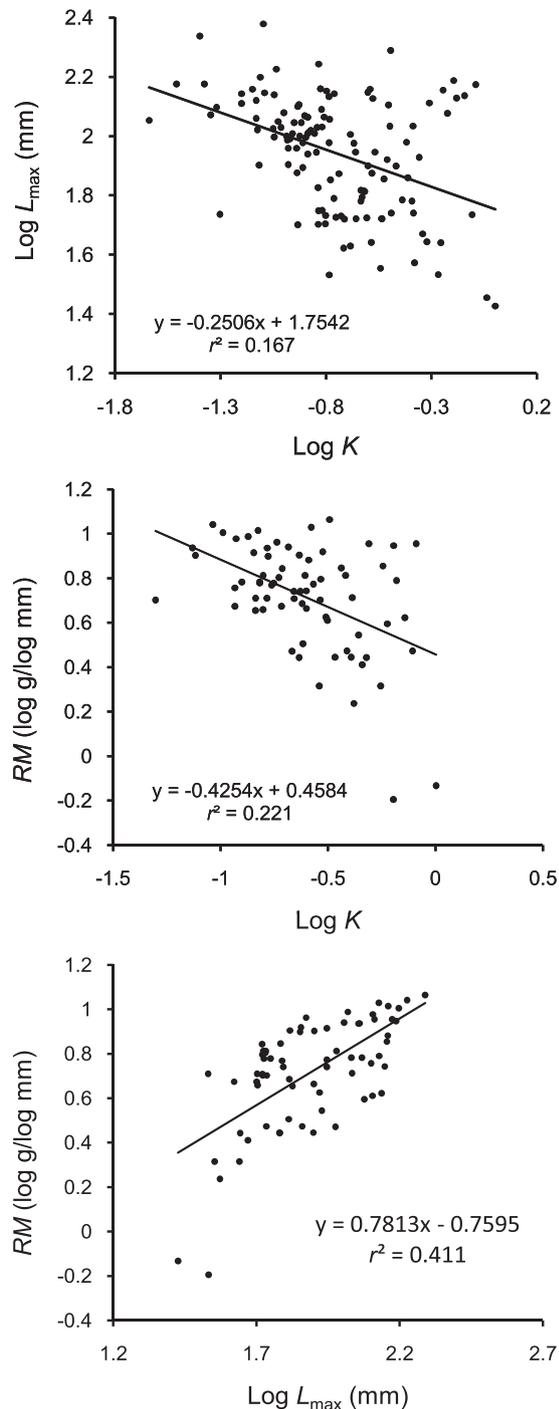


Fig. 6. Relationships among growth variables of freshwater mussels. K is the von Bertalanffy growth constant, L_{\max} is maximum observed length, and RM is relative shell mass expressed as \log mass/ \log length (g mm^{-1}). All regressions are significant at $P < 0.0001$.

Most surprising was our finding of a slow-growing, dwarfed form of *Quadrula asperata* coexisting with the normal growth form in the Sipsey River. Slow-growing individuals of *Q. asperata* were rare in the Sipsey River. Out of a total

of 163 individuals measured initially in the Sipsey River (all sites combined), only five (3%) were of the slow-growing form. We later searched through other specimens and found five more slow-growing individuals; all slow-growing individuals occurred at a single site and were not found elsewhere in the river or in any other river. A possible explanation for this alternative growth form is that it represents a separate species. This seems unlikely because, other than growth rate and size, slow-growing individuals were indistinguishable from individuals exhibiting normal growth. Furthermore, there is no reported polytypy in shell morphology or other evidence of cryptic species contained within *Q. asperata* in the western Mobile Basin (Williams, Bogan & Garner, 2008).

Freshwater mussels often experience injuries to the shell or mantle that result in reduced growth thereafter (Coker *et al.*, 1921; Haag & Commens-Carson, 2008). We observed no evidence of past injuries in slow-growing individuals of *Q. asperata*; rather, this alternative growth trajectory appears to be established early and maintained throughout life (see Fig. 4). In many organisms, stunted or dwarfed populations occur frequently due to resource limitation (e.g. trees on poor sites, fish in overcrowded ponds) and stunted populations of mussels have been reported (Clark & Wilson, 1912; Clarke & Stansbery, 1988; Kesler *et al.*, 2007). However, growth polymorphism within a single population has not been reported previously in mussels and is known in few other organisms. Polymorphisms in growth and size are known in male sunfishes (*Lepomis* spp.), male salmon (*Oncorhynchus* spp.), and in *Maculinea* spp. butterfly larvae, and are considered to represent alternative fitness-maximizing life-history strategies (Gross, 1982, 1985; Thomas, Elmes & Wardlaw, 1998). The potential adaptive value of the slow-growing form of *Q. asperata* is unknown but it is associated with greatly increased life span suggesting that divergent life histories may occur within as well as among mussel populations.

(2) Growth and mussel life histories

The variation in age and growth at all levels suggests that energy allocation to growth in mussels is highly plastic and associated with fundamental physiological and evolutionary trade-offs. A high percentage of observed variation in longevity was explained by the negative relationship between longevity and the growth rate, K , even when accounting for effects of phylogeny. By contrast, path analysis indicated that size (L_{\max}) had no significant direct effect on longevity. Although relative shell mass had a significant positive effect on longevity, much of this relationship is due to the indirect effect of K on shell mass. Overall, species with higher growth rates invested less energy in production of shell material, having smaller and less massive shells than species with slower growth. However, the growth rate, K , explained little of the variation in shell length and mass, especially when corrected for phylogeny (length only), and path analysis showed that K has little direct effect on length; rather, increased investment to shell material in species with slower growth occurs mainly as a steady increase in shell mass over their proportionally longer life spans. These results suggest that, although length

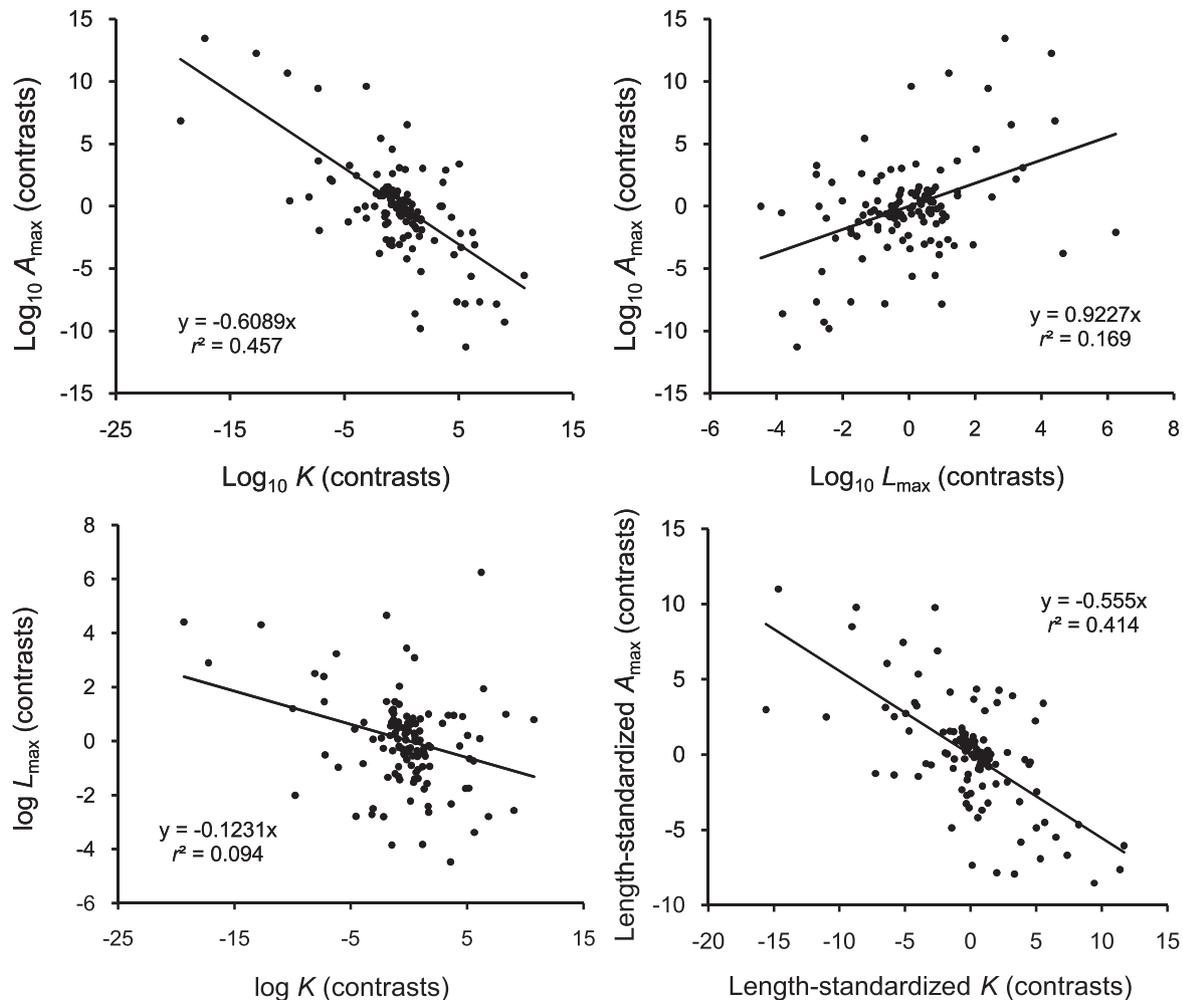


Fig. 7. Relationships between phylogenetically independent contrasts for age and growth variables of freshwater mussels. A_{\max} is maximum observed longevity, K is the von Bertalanffy growth constant, and L_{\max} is maximum observed length. Length-standardized variables (lower right panel) are residuals of \log_{10} -transformed values regressed on \log_{10} length. All regression lines pass through the origin and all are significant at $P < 0.001$.

and mass may vary in response to environmental factors, energy investment in shell material has little influence on longevity. With regard to age and growth, differential patterns of energy allocation are manifested primarily as a trade-off between longevity and growth rate.

The negative relationship between longevity and growth rate has been shown previously for mussels among populations of *Margaritifera margaritifera* (Bauer, 1992), *Unio crassus* (Hochwald, 2001), and *Anodonta piscinalis* (Haukioja & Hakala, 1978), as well as in fishes (Metcalf & Monaghan, 2003), lizards (Olsson & Shine, 2002), and mammals (White & Seymour, 2004), suggesting that this is a general phenomenon. Physiological mechanisms of ageing centre on the rate of living hypothesis and its molecular mechanism, the free radical theory of ageing, which state that faster growth or energy expenditure is associated with shorter life span due to increased oxidative stress and other cellular damage (Beckman & Ames, 1998; Bonsall, 2005). In an

evolutionary context, the concept of the fast-slow continuum in life histories describes relative patterns of energy allocation among traits and the selective pressures that produce them (Read & Harvey, 1989; Promislow & Harvey, 1990; Bielby *et al.*, 2007). A “slow” life history is characterized by a longer life span due to increased energy investment in production of a durable soma and repair of somatic damage at the expense of later and lower investment in reproduction and growth, and this strategy is expected to be favoured under conditions of low extrinsic mortality (Kirkwood, 1990; Arendt, 1997; Cichon, 1997). Physiological constraints imposed upon the allocation of limited resources will preclude certain combinations of life-history traits (for example, fast growth and long life) causing these traits to covary in predictable ways (Ricklefs & Wikelski, 2002).

The strong and pervasive relationship between growth rate and longevity in mussels suggests that growth rate is a valuable proxy for the “speed” of a life history (i.e. its

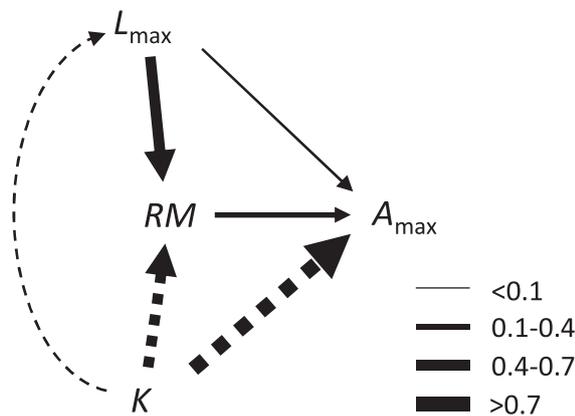


Fig. 8. Path diagram for the effect of growth variables on freshwater mussel longevity. Positive effects are indicated by solid lines and negative effects are indicated by dashed lines. The legend gives the approximate magnitude of direct effects. See Table 5 for actual values and significance levels. A_{\max} is maximum observed age (years); L_{\max} is maximum observed length (mm); RM is relative shell mass; K is the von Bertalanffy growth constant.

position along the fast-slow continuum) and therefore may be predictive of other life history traits. Limited observations for mussels support an association between fast growth and greater and earlier investment in reproduction. Females in faster-growing populations of *Amblema plicata* in the Little Tallahatchie River produce more glochidia than in slower-growing populations in the Sipsy River (Haag & Staton, 2003) and faster-growing populations of *Unio crassus* spawned more frequently than slower-growing populations (Hochwald, 2001). Similarly, *Anodonta piscinalis* from more productive habitats (and with higher growth) had higher reproductive output than mussels from poorer habitats (Jokela & Mutikainen, 1995), and reproductive investment was negatively correlated with life span but positively correlated with growth (Haukioja & Hakala, 1978). In fishes, age at maturity is negatively related to growth rate (He & Stewart, 2002), but this relationship has not been tested for mussels. In most species, we observed an abrupt decline in growth occurring within the first 10 years of an individual growth chronology. This inflection point may reflect

diversion of resources from growth to reproduction, allowing estimation of age at maturity based on growth parameters (Dunca & Mutvei, 2001; He & Stewart, 2002). Fast-growing species (e.g. *Lampsilis ornata*) have been reported to mature as early as their first year while slow-growing species (e.g. *Cyclonaias tuberculata*, *Quadrula asperata*, *Q. pustulosa*, *Margaritifera margaritifera*) do not mature until 5–20 years (Bauer, 1987; Jirka & Neves, 1992; Haag & Staton, 2003). The degree to which these apparent trade-offs among life-history traits are adaptive remains unknown, but predictions from life-history theory provide a powerful framework for testing ideas about life-history evolution in mussels.

Little is known about selective forces that may influence patterns of energy allocation in mussels. High extrinsic mortality is thought to favour fast growth and short life spans because organisms must quickly reach reproductive age (Arendt, 1997; Cichon, 1997). Mussels are typically characterized as having low natural mortality (e.g. Hart *et al.*, 2001), but like previous generalizations about age and growth, this notion may underestimate the variability in this trait. The few existing data suggest that mortality may be highly variable across populations and age classes (Jokela & Mutikainen, 1995; Villella, Smith & Lemarie, 2004) and allocation of energy to growth and reproduction may vary under different levels of mortality (Jokela & Mutikainen, 1995). Life-history theory predicts that mussel species with fast growth and short life spans (e.g. *Leptodea fragilis*, *Medionidus acutissimus*, *Toxolasma spp.*) will have mortality rates much higher than those typically reported for long-lived species (e.g. *Amblema plicata*; Hart *et al.*, 2001). Consequently, variation in mortality among species and populations should be expected to be comparable to that seen in age and growth.

In addition to differences among populations due to site-specific factors, plasticity of mussel growth is demonstrated in response to changes in environmental conditions. In transplant experiments, mussel growth varied widely among transplant sites, showing little influence of site of origin (Jokela & Mutikainen, 1995; Kesler & Van Tol, 2000) and in one study, transplanted mussels quickly assumed growth characteristics similar to resident individuals at transplant sites (Kesler *et al.*, 2007). Streams affected by cold, hypolimnetic discharge from reservoirs often have relict mussel assemblages composed of individuals that recruited prior to dam

Table 5. Path coefficients from linear regression of freshwater mussel growth variables, and decomposition of correlations. Direct effects are the path coefficients appearing in Fig. 8. The effect coefficient is the sum of the two effect components and represents the total effect of an independent variable. A_{\max} is maximum observed age (years); L_{\max} is maximum observed length (mm), K is the von Bertalanffy growth rate. * $P < 0.05$, *** $P < 0.0001$, ns = not significant

Dependent variable	Model r^2	Independent variables	Direct effect	Indirect effect	Effect coefficient
A_{\max}	0.797	K	-0.760***	-0.109	-0.869
		L_{\max}	0.016 ^{ns}	0.133	0.149
		Relative shell mass	0.215*	0	0.215
Relative shell mass	0.634	K	-0.434***	-0.397	-0.831
		L_{\max}	0.619***	0	0.619
L_{\max}	0.013	K	-0.114 ^{ns}	0	-0.114

construction and individuals may reach ages exceeding maximum longevity reported for those species in other streams. Although growth rates in these habitats have not been determined, growth rings are tightly crowded and shells become more massive than in other streams (Parmalee, Klippel & Bogan, 1980), suggesting that depressed growth rates due to low water temperature facilitate attainment of maximum ages beyond the normal range for these species.

We were unable to measure age and growth in only a single species, *Unio tetrasmus*. This species is one of the few that can withstand lengthy periods of desiccation (Holland, 1991). In marine bivalves, desiccation results in formation of rings due to greater conchiolin deposition during anaerobic metabolism (Lutz & Rhoads, 1977), and this phenomenon probably explains the proliferation of rings we observed in *U. tetrasmus*. Patterns of shell rings in this species may provide a record of hydrological cycles in ephemeral aquatic habitats.

(3) Implications for mussel conservation and management

The great variation in age and growth of freshwater mussels shows that these animals employ a diverse array of life-history strategies requiring vastly different conservation and management approaches. Management approaches and monitoring criteria developed under the assumption of slow growth and long life for mussels may be wholly inappropriate for short-lived species. Life-history theory predicts that species with fast growth and short life spans are adapted to variable environments and can sustain higher mortality but require higher recruitment than species adapted to constant environments (Winemiller & Rose, 1992). Because of the rapid generation time of short-lived species they may also be expected to respond more quickly to environmental changes whether due to habitat degradation or restoration. Although age and growth is constrained to some extent by phylogeny, phenotypic plasticity within species further suggests that management approaches may need to be tailored to specific populations to account for large differences in growth rate, longevity, and other life-history traits.

There may even be growth differences within populations that require management consideration. For example, we found significant differences in growth between sexes in several species. Commercial harvest size limits determined without accounting for sex-specific growth may result in unintended differences in mortality between sexes. Distortion of sex ratios due to unequal harvest can lead to Allee effects by reducing the probability of individuals finding mates (Fogarty & O'Brien, 2009); this problem was implicated in the crash of the yellow perch (*Perca flavescens*) population in the Great Lakes in the 1990s (Wilberg *et al.*, 2005). Most species for which we observed sex-specific differences in growth are not harvested commercially (e.g. *Obovaria jacksoniana*, *O. unicolor*, *Toxolasma texasensis*, *Villosa spp.*). Nevertheless, the existence of sex-specific and other within-population variation in growth (e.g. fast and slow growth forms in *Quadrula asperata*) means that different subsets of a population can be expected to respond differently to management in some cases.

Determination of age and growth for a population of interest should be considered a prerequisite for freshwater mussel management as it is for management of other fisheries resources (e.g. DeVries & Frie, 1996; Campana & Thorrold, 2001). In addition to revealing potentially important within-population variation, age and growth studies are necessary because latitudinal and other environmental influences preclude generalization of existing growth data from other populations. For example, although shell size is generally positively related to age within a population, across populations size was a poor predictor of age even within species. In many cases, populations with larger maximum size had considerably lower longevity (e.g. *Quadrula asperata*, *Truncilla truncata*). Populations with different growth rates, maximum size, and longevity will also likely differ in other important life-history traits including size at maturity, fecundity, and mortality. Applying existing growth data from other populations will often result in inaccurate demographic conclusions about a study population, leading to potentially ineffective or harmful management strategies.

V. CONCLUSIONS

- (1) The frequent depiction of freshwater mussels as “long-lived and slow-growing” is not an accurate generalization for this group. Although many species do grow slowly and reach advanced ages, other species grow surprisingly fast and have short life spans. Maximum ages of long-lived mussel species greatly exceed those of many invertebrates, but other mussel species have life spans similar to some invertebrate groups such as decapods, crustaceans and echinoderms; overall, the range of longevities for mussels is similar to vertebrates (e.g. Hulbert *et al.*, 2007). In our original and compiled data set, longevity of freshwater mussels spanned nearly two orders of magnitude, ranging among species from four years to nearly 200 years, and values of the growth constant, K , spanned a similar range (0.02–1.01). This range is similar to marine bivalves in which longevity ranges from about one year to over 200 years (Heller, 1990). Like marine bivalves, the apparent great diversity in life-history strategies of freshwater mussels defies attempts to make generalizations about age and growth for the group as a whole.
- (2) Patterns of age and growth are fundamental to understanding mussel life-history evolution and diversification. The growth rate, K , is an important indicator of the amount of energy allocated to growth *versus* other functions, and K describes this allocation more accurately than does shell size or mass. In addition to influencing longevity, growth rate is probably predictive of other life-history variables and may reflect responses to environmental factors. The great variation in growth and longevity suggests that mussel species have divergent life histories encompassing a broad cross section of the fast-slow continuum. Future

studies assessing how variation in fecundity, mortality, and other life-history variables covary with growth will describe more fully the diversity of mussel life histories and will help to understand the role of these strategies in the taxonomic radiation of this group.

- (3) Differences in growth and longevity among species have important conservation and management implications. Conservation approaches developed under the assumption of slow growth and long life will be inappropriate for many species. In addition, because there can be substantial intraspecific variation in growth, generalizing growth data for a particular population to others can lead to erroneous conclusions about population dynamics and expected responses to management. Therefore, we recommend that future population studies incorporate only growth data derived from the study population itself and not from existing data on other populations.
- (4) Additional research will undoubtedly refine our estimates of maximum life span for many mussel species and show an even greater range of variability in age and growth among populations. Because most of our populations were from the southern U.S., northern populations should be expected to have slower growth rates and greater longevity (e.g. Bauer 1992; Hochwald, 2001). Furthermore, several of our populations are represented by small sample sizes and examination of more individuals would likely increase our estimates of maximum life span. Nevertheless, the tight relationship we observed between longevity and K , as well as our focus on obtaining large individuals from these populations, supports that these are reasonable approximations of maximum longevity for our study populations.
- (5) With the exception of one species (*Unio tetrallasmus*) from ephemeral habitats, all species in our study provided interpretable shell rings that cross-dating showed to be reliable indicators of age and growth. Analysis of shell rings offers almost limitless and largely untapped opportunities for investigating patterns of age and growth in freshwater mussels. Furthermore, by incorporating historical and archaeological material in addition to contemporary specimens, growth rings can provide a valuable record of past environmental conditions.

VI. ACKNOWLEDGEMENTS

We thank the following people for their various contributions to this study. Mickey Bland expertly prepared hundreds of shell thin sections and assisted with specimen collection and interpretation of shell rings. Amy Commens-Carson, Gordon McWhirter, Leann Staton, and Angela Greer also assisted with field and laboratory work. David Campbell provided a phylogeny of freshwater mussels. Jeff Garner, Mark Hove, and John Harris provided specimens for age and growth analysis. Mel Warren and Tom Dell made helpful comments

on the manuscript. This study was supported by the Southern Research Station, U.S. Forest Service.

VII. REFERENCES

- ALDRIDGE, D.C. (1999). The morphology, growth and reproduction of Unionidae (Bivalvia) in a Fenland waterway. *Journal of Molluscan Studies* **65**, 47–60.
- ANTHONY, J.L., KESLER, D.H., DOWNING, W.L. & DOWNING, J.A. (2001). Length-specific growth rates in freshwater mussels (Bivalvia: Unionidae): extreme longevity or generalized growth cessation? *Freshwater Biology* **46**, 1349–1359.
- ARENDT, J.D. (1997). Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology* **72**, 149–177.
- BACHELET, G. (1980). Growth and recruitment of the tellinid bivalve *Macoma balthica* at the southern limit of its geographical distribution, the Gironde estuary (SW France). *Marine Biology* **59**, 105–117.
- BAILEY, R.C. & GREEN, R.H. (1988). Within-basin variation in the shell morphology and growth rate of a freshwater mussel. *Canadian Journal of Zoology* **66**, 1704–1408.
- BAIRD, M.S. (2000). *Life history of the spectaclecase, Cumberlandia monodonta Say, 1829 (Bivalvia, Unionoidea, Margaritiferidae)*. M.S. THESIS. Southwest Missouri State University, Springfield.
- BAUER, G. (1987). Reproductive strategy of the freshwater pearl mussel *Margaritifera margaritifera*. *Journal of Animal Ecology* **56**, 691–704.
- BAUER, G. (1992). Variation in the life span and size of the freshwater pearl mussel. *Journal of Animal Ecology* **61**, 425–436.
- BECKMAN, K.B. & AMES, B.N. (1998). The free radical theory of ageing matures. *Physiological Review* **78**, 547–581.
- BENNETT, P.M. & OWENS, I.P.F. (1997). Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceeding of the Royal Society of London B* **264**, 401–408.
- BIELBY, J., MACE, G.M., BININDA-EMONDS, O.R., CARDILLO, M., GITTLEMAN, J.L., JONES, K.E., ORME, C.D. & PURVIS, A. (2007). The fast-slow continuum in mammalian life history: an empirical reevaluation. *The American Naturalist* **169**, 748–757.
- BLACK, B.A., BOEHLERT, G.W. & YOKLAVICH, M.M. (2005). Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes. *Canadian Journal of Fisheries and Aquatic Science* **62**, 2277–2284.
- BLACK, B.A., DUNHAM, J., BLUNDON, B.W., RAGGON, M. & ZIMA, D. (in press). Spatial variability in growth-increment chronologies of long-lived freshwater mussels: implications for climate impacts and reconstructions. *Ecoscience*.
- BOGAN, A.E. (2008). Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater. *Hydrobiologia* **595**, 139–147.
- BONSALL, M.B. (2005). Longevity and ageing: appraising the evolutionary consequences of growing old. *Philosophical Transactions of the Royal Society of London B* **361**, 119–135.
- BRUENDERMAN, S.A., & NEVES, R.J. (1993). Life history of the endangered fine-rayed pigtoe, *Fusconaia cuneolus* (Bivalvia: Unionidae) in the Clinch River, Virginia. *American Malacological Bulletin* **10**, 83–91.
- CALDER, W.A. (1984). *Size, Function and Life History*, Harvard University Press, Boston.
- CAMPANA, S.E. & THORROLD, S.R. (2001). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Science* **58**, 30–38.
- CAMPBELL, D.C., SERB, J.M., BUHAY, J.E., ROE, K.J., MINTON, R.L. & LYDEARD, C. (2005). Phylogeny of North American amblymines (Bivalvia, Unionoidea): prodigious polyphyly proves pervasive across genera. *Invertebrate Biology* **124**, 131–164.
- CHARNOV, E.L. (1993). *Life History Invariants*, Oxford University Press, Oxford, UK.
- CHRISTIAN, A.D., DAVIDSON, C.L., POSEY, W.R., RUST, P.J., FARRIS, J.L., HARRIS, J.L. & HARP, G.L. (2000). Growth curves of four species of commercially valuable freshwater mussels (Bivalvia: Unionidae) in Arkansas. *Journal of the Arkansas Academy of Science* **54**, 41–50.
- CICHON, M. (1997). Evolution of longevity through optimal resource allocation. *Philosophical Transactions of the Royal Society of London B* **264**, 1383–1388.
- CLARK, G.R. (1980). Study of molluscan shell structure and growth lines using thin sections. In: *Skeletal growth in aquatic organisms*. (eds D.C. RHOADS and R.A. LUTZ), pp. 603–614. Plenum Press, New York, New York.
- CLARK, H.W. & WILSON, C.B. (1912). The mussel fauna of the Maumee River. *Bureau of Fisheries* **757**, 1–72.
- CLARKE, A.H. & STANSBURY, D.H. (1988). Are some Lake Erie mollusca products of post-Pleistocene evolution? In: *The biogeography of the island region of western Lake Erie*. (ed. J.F. DOWNHOWER), pp. 85–274. Ohio State University Press, Columbus.
- COKER, R. E., SHIRA, A. F., CLARK, H. W. & HOWARD, A. D. (1921). Natural history and propagation of fresh-water mussels. *Bulletin of the Bureau of Fisheries*, **37**, 79–181.
- COOK, E. R. & HOLMES, R. L. (1984). *Program ARSTAN and users manual*, Lamont Doherty Geological Observatory, Palisades, New York.

- DENNIS, B., MUNHOLLAND, P.L. & SCOTT, J.M. (1991). Estimation of growth and extinction parameters for endangered species. *Ecological Monographs*, **61**, 115–143.
- DEVRIES, D. & FRIE, R. (1996). Determination of age and growth. In: *Fisheries Techniques*. (Eds B. MURPHY and D. WILLIS). American Fisheries Society, Bethesda.
- DUNCA, E. & MUTVEI, H. (2001). Comparison of microgrowth patterns in *Margaritifera margaritifera* shells from south and north Sweden. *American Malacological Bulletin*, **16**, 239–250.
- FELSENSTEIN, J. (1985). Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.
- FELSENSTEIN, J. (2005). *PHYLIP (Phylogeny Inference Package) version 3.6*. Distributed by the author. Department of Genome Sciences, University of Washington, Seattle. Available at: <http://evolution.genetics.washington.edu/phylip.html>.
- FOGARTY, M.J. & O'BRIEN, L. (2009). Recruitment in marine fish populations. In: *Fish Reproductive Biology: Implications for Assessment & Management*. (Eds T. JACKSON, M. FOGARTY, B. A. MEGREY, and E. MOKSNESS). Wiley, Malaysia.
- GARLAND, T., JR., HARVEY, P.H. & IVES, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *American Naturalist*, **41**, 18–32.
- GRAF, D.L. & CUMMINGS, K.S. (2007). Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). *Journal of Molluscan Studies*, **73**, 291–314.
- GRIFFITHS, N.A. & CYR, H. (2006). Are there hot spots for *Elliptio complanata* in the shallow littoral zone of a large Canadian Shield lake? *Canadian Journal of Fisheries and Aquatic Science*, **63**, 2137–2147.
- GRIME, J.P. (1997). *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. John Wiley & Sons, Ltd., Chichester.
- GRISSINO-MAYER, H.D. (2001). Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research*, **57**, 205–221.
- GROSS, M.R. (1982). Sneakers, satellites, and parental–polymorphic mating strategies in North American sunfishes. *Zeitschrift für Tierpsychologie*, **60**, 1–26.
- GROSS, M.R. (1985). Disruptive selection for alternative life histories in salmon. *Nature*, **313**, 47–48.
- HAAG, W.R. (2009). Extreme longevity in freshwater mussels revisited: sources of bias in age estimates derived from mark-recapture experiments. *Freshwater Biology*, **54**, 1474–1486.
- HAAG, W.R. & COMMENS-CARSON, A.M. (2008). Testing the assumption of annual shell ring deposition in freshwater mussels. *Canadian Journal of Fisheries and Aquatic Science*, **65**, 493–508.
- HAAG, W.R. & STATON, J.L. (2003). Variation in fecundity and other reproductive traits in freshwater mussels. *Freshwater Biology*, **48**, 2118–2130.
- HANLON, S.D. & LEVINE, J.F. (2004). Notes on the life history and demographics of the Savannah lilliput (*Toxolasma pullus*) (Bivalvia: Unionidae) in University Lake, NC. *Southeastern Naturalist*, **3**, 289–296.
- HANSON, J.M., MACKAY, W.C. & PREPAS, E.E. (1988). The effects of water depth and density on the growth of a unionid clam. *Freshwater Biology*, **19**, 345–355.
- HART, R.A., GRIER, J.W., MILLER, A.C. & DAVIS, M. (2001). Empirically derived survival rates of a native mussel, *Amblema plicata*, in the Mississippi and Otter Tail Rivers, Minnesota. *American Midland Naturalist*, **146**, 254–263.
- HASTIE, L.C., BOON, P.J. & YOUNG, M.R. (2000). Physical microhabitat requirements of freshwater pearl mussels, *Margaritifera margaritifera* (L.). *Hydrobiologia*, **429**, 59–71.
- HAUKIOJA, E. & HAKALA, T. (1978). Measuring growth from shell rings in populations of *Anodonta piscinalis* (Pelecypoda, Unionidae). *Annales Zoologici Fennici*, **15**, 60–65.
- HE, J.X. & STEWART, D.J. (2002). A stage-explicit expression of the von Bertalanffy growth model for understanding age at first reproduction of Great Lakes fishes. *Canadian Journal of Fisheries and Aquatic Science*, **59**, 250–261.
- HELAMA, S. & VALOVIRTA, I. (2008). Ontogenetic morphometrics of individual freshwater pearl mussels (*Margaritifera margaritifera* (L.)) reconstructed from geometric conchology and trigonometric sclerochronology. *Hydrobiologia*, **610**, 43–53.
- HELLER, J. (1990). Longevity in molluscs. *Malacologia*, **31**, 259–295.
- HINCH, S.G., BAILEY, R.C. & GREEN, R.H. (1986). Growth of *Lampsilis radiata* (Bivalvia: Unionidae) in sand and mud: A reciprocal transplant experiment. *Canadian Journal of Fisheries and Aquatic Science*, **43**, 548–552.
- HINCH, S.G., KELLY, L.J. & GREEN, R.H. (1989). Morphological variation of *Elliptio complanata* (Bivalvia: Unionidae) in differing sediments of soft-water lakes exposed to acidic deposition. *Canadian Journal of Zoology*, **67**, 1895–1899.
- HOCHWALD, S. (2001). Plasticity of life-history traits in *Unio crassus*. In: *Ecology and evolution of the freshwater mussels Unionoida*. (eds K. BAUER and K. WÄCHTLER), pp. 127–142. Ecological Studies, Vol. 145. Springer-Verlag, Berlin.
- HOLLAND, D.F. (1991). *Prolonged emersion tolerance in freshwater mussels (Bivalvia: Unionidae): interspecific comparison of behavioral strategies and water loss rates*. M.S. THESIS, The University of Texas at Arlington, Arlington.
- HOLMES, R.L. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, **43**, 69–75.
- HOVE, M.C. & NEVES, R.J. (1994). Life history of the endangered James spinymussel *Pleurobema collina* (Conrad, 1837) (Mollusca: Unionidae). *American Malacological Bulletin*, **11**, 29–40.
- HOWARD, J.K. & CUFFEY, K.M. (2006). Factors controlling the age structure of *Margaritifera falcata* in 2 northern California streams. *Journal of the North American Benthological Society*, **25**, 677–690.
- HULBERT, A.J., PAMPLONA, R., BUFFENSTEIN, R. & BUTTEMER, W.A. (2007). Life and death: metabolic rate, membrane composition, and life span of animals. *Physiological Reviews*, **87**, 1175–1213.
- 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*. M.S. THESIS. Virginia Polytechnic Institute and State University, Blacksburg.
- JIRKA, K.J. & NEVES, R.J. (1992). Reproductive biology of four species of freshwater mussels (Mollusca: Unionidae) in the New River, Virginia and West Virginia. *Journal of Freshwater Ecology*, **7**, 35–44.
- JOKELA, J. & MUTIKAINEN, P. (1995). Phenotypic plasticity and priority rules for energy allocation in a freshwater clam: A field experiment. *Oecologia*, **104**, 122–132.
- JONES, J.W. & NEVES, R.J. (2002). Life history and propagation of the endangered fanshell pearly mussel, *Cyprogenia stegaria* Rafinesque (Bivalvia: Unionidae). *Journal of the North American Benthological Society*, **21**, 76–88.
- JONES, J.W., NEVES, R.J., AHLSTEDT, S.A. & MAIR, R.A. (2004). Life history and propagation of the endangered dromedary pearly mussel (*Dromus dromas*) (Bivalvia: Unionidae). *Journal of the North American Benthological Society*, **23**, 515–525.
- KESLER, D.H. & VAN TOL, N. (2000). Growth of the freshwater mussel, *Pyganodon Grandis* (Unionidae) in two west Tennessee borrow pits. *Journal of the Tennessee Academy of Science*, **75**, 71–75.
- KESLER, D.H., NEWTON, T.J. & GREEN, L. (2007). Long-term monitoring of growth in the eastern Elliptio, *Elliptio complanata* (Bivalve: Unionidae), in Rhode Island: a transplant experiment. *Journal of the North American Benthological Society*, **26**, 123–133.
- KIMURA, D.K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*, **77**, 765–776.
- KIRKWOOD, T.B.L. (1990). The disposable soma theory of ageing. In: *Genetic effects on ageing*. (ed. D.E. HARRISON), pp. 9–19. Telford Press, Caldwell, NJ.
- LUTZ, R.A. & RHOADS, D.C. (1977). Anaerobiosis and theory of growth line formation. *Science*, **198**, 1222–1227.
- MACKIE, G.L. & FLIPPANCE, L.A. (1983). Relationships between buffering capacity of water and the size and calcium content of freshwater mollusks. *Freshwater Invertebrate Biology*, **2**, 48–55.
- MCMAHON, R.F. & BOGAN, A.E. (2001). Mollusca: Bivalvia. In: *Ecology and classification of North American freshwater invertebrates*. (eds J.H. THORP and A.P. COVICH), pp. 321–429. Academic Press, San Diego.
- METCALFE, N.B. & MONAGHAN, P. (2003). Growth versus lifespan: perspectives from evolutionary ecology. *Experimental Gerontology*, **38**, 935–940.
- MICHAELSON, D.L. & NEVES, R.J. (1995). Life history and habitat of the endangered dwarf wedgemussel *Alasmodonta heterodon* (Bivalvia: Unionidae). *Journal of the North American Benthological Society*, **14**, 324–340.
- MOLES, K.R. & LAYZER, J.B. (2008). Reproductive ecology of *Actinonaias ligamentina* (Bivalvia: Unionidae) in a regulated river. *Journal of the North American Benthological Society*, **27**, 212–222.
- MORRIS, T.J. & CORKUM, L.D. (1999). Unionid growth patterns in rivers of differing riparian vegetation. *Freshwater Biology*, **42**, 58–68.
- NDUKU, W.K. & HARRISON, A.D. (1976). Calcium as a limiting factor in the biology of *Biomphalaria pfeifferi* (Krauss) (Gastropoda: Planorbidae). *Hydrobiologia*, **49**, 143–170.
- NEVES, R.J. & MOYER, S.N. (1988). Evaluation of techniques for age determination of freshwater mussels (Unionidae). *American Malacological Bulletin*, **6**, 179–188.
- NEVES, R.J., BOGAN, A.E., WILLIAMS, J.D., AHLSTEDT, S.A. & HARTFIELD, P.W. (1997). Status of aquatic mollusks in the southeastern United States: A downward spiral of diversity. In: *Aquatic Fauna in Peril: The Southeastern Perspective*. (eds G.W. BENZ and D.E. COLLINS), pp. 43–86. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design and Communications, Decatur, GA.
- NICHOLS, F.H. & THOMPSON, J.K. (1982). Seasonal growth in the bivalve *Macoma ballhica* near the southern limit of its range. *Estuaries*, **5**, 110–120.
- OLSSON, M. & SHINE, R. (2002). Growth to death in lizards. *Evolution*, **56**, 1867.
- OSTROVSKY, L., GOPHEN, M. & KALIKHMAN, I. (1993). Distribution, growth, production, and ecological significance of the clam *Unio terminalis* in Lake Kinneret, Israel. *Hydrobiologia*, **271**, 49–63.
- PARMALEE, P.W., KLIPPEL, W.E. & BOGAN, A.E. (1980). Notes on the prehistoric and present status of the naiaid fauna of the Middle Cumberland River, Smith county, Tennessee. *The Nautilus*, **94**, 93–104.
- PATERSON, C.G. (1985). Biomass and production of the unionid, *Elliptio complanata* (Lightfoot) in an old reservoir in New Brunswick, Canada. *Freshwater Invertebrate Biology*, **4**, 201–207.
- PROMISLOW, D.E.L. & HARVEY, P.H. (1990). Living fast and dying young: a comparative analysis of life-history variation among mammals. *Journal of Zoology*, **220**, 417–437.
- READ, A.F. & HARVEY, P.H. (1989). Life history differences among the eutherian radiations. *Journal of Zoology*, **219**, 329–353.
- REGNIER, C., FONTAINE, B. & BOUCHET, P. (2009). Not knowing, not recording, not listing: numerous unnoticed mollusk extinctions. *Conservation Biology*, **23**, 1214–1221.
- RICKER, W.E. (1975). Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin*, **191**, 382.

- RICKLEFS, R.E. & WIKELSKI, M. (2002). The physiology/life history nexus. *Trends in Ecology and Evolution*, **17**, 462–468.
- ROLLO, C.D. (2002). Growth negatively impacts the life span of mammals. *Evolution and Development*, **4**, 55–61.
- RYPEL, A.L., HAAG, W.R. & FINDLAY, R.H. (2008). Validation of annual growth rings in freshwater mussel shells using crossdating. *Canadian Journal of Fisheries and Aquatic Science*, **65**, 2224–2232.
- RYPEL, A.L., HAAG, W.R. & FINDLAY, R.H. (2009). Pervasive hydrologic effects on freshwater mussels and riparian trees in southeastern floodplain ecosystems. *Wetlands*, **29**, 497–504.
- SAN MIGUEL, E., MONSERRAT, S., FERNANDEZ, C., AMARO, R., HERMIDA, M., ONDINA, P. & ALTABA, C.R. (2004). Growth models and longevity of freshwater pearl mussels (*Margaritifera margaritifera*) in Spain. *Canadian Journal of Zoology*, **82**, 1370–1379.
- SAS (2002–2003). SAS for Windows, version 9.1. Cary, North Carolina.
- SCHEMSKE, D.W. & HORVITZ, C. (1988). Plant-animal interactions and fruit production in a neotropical herb: a path analysis. *Ecology*, **69**, 1128–1137.
- SCHLUTER, D. (2000). *The Ecology of Adaptive Radiation*, Oxford University Press, Oxford.
- SCHÖNE, B.R., DUNCA, E., MUTVEI, H. & NORLUND, U. (2004). A 217-year record of summer air temperature reconstructed from freshwater pearl mussel (*M. margaritifera*, Sweden). *Quaternary Science Review*, **23**, 1803–1816.
- SERB, J.M., BUHAY, J. E. & LYDEARD, C. (2003). Molecular systematics of the North American freshwater bevalve genus *Quadrula* (Unionidae: Ambleminae) based on mitochondrial ND1 sequences. *Molecular Phylogenetics and Evolution*, **28**, 1–11.
- SOKAL, R.R. & ROHLF, F.J. (1995). *Biometry*, W. H. FREEMAN, New York.
- ST. JOHN, M.E. (1973). *Shell growth and variation in the Actinonaias ligamentina (Lamarck, 1819) complex (Mollusca: Bivalvia: Unionidae)*. Ph.D. Thesis. The Ohio State University, Columbus.
- STANSBERRY, D.H. (1967). Growth and longevity of naiades from Fishery Bay in Western Lake Erie. *American Malacological Union, Inc. Annual Reports*, **34**, 10–11.
- STEARNS, S.C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, **41**, 173–187.
- STOBER, Q.J. (1972). Distribution and age of *Margaritifera margaritifera* (L.) in a Madison River (Montana, U.S.A.) mussel bed. *Malacologia*, **11**, 343–350.
- STRAYER, D.L., COLE, J.J., LIKENS, G.E. & BUSO, D.C. (1981). Biomass and annual production of the freshwater mussel *Elliptio complanata* in an oligotrophic softwater lake. *Freshwater Biology*, **11**, 435–440.
- STRAYER, D.L., CARACO, N.F., COLE, J.J., FINDLAY, S. & PACE, M.L. (1999). Transformation of freshwater ecosystems by bivalves. *BioScience*, **49**, 19–27.
- STRAYER, D.L., DOWNING, J.A., HAAG, W.R., KING, T.L., LAYZER, J.B., NEWTON, T.J. & NICHOLS, S.J. (2004). Changing perspectives on pearly mussels, America's most imperiled animals. *BioScience*, **54**, 429–439.
- THOMAS, J.A., ELMES, G.W. & WARDLAW, J.C. (1998). Polymorphic growth in larvae of the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Philosophical Transactions of the Royal Society of London B*, **265**, 1895–1901.
- VALDOVINOS, C. & PEDREROS, P. (2007). Geographic variations in shell growth rates of the mussel *Diplodon chilensis* from temperate lakes of Chile: Implications for biodiversity conservation. *Limnologia*, **37**, 63–75.
- VANNOTE, R.L. & MINSHALL, G.W. (1982). Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. *Proceedings of the National Academy of Science*, **79**, 4103–4107.
- VAUGHN, C.C. & HAKENKAMP, C.C. (2001). The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology*, **46**, 1431–1446.
- VEINOTT, G.I. & CORNETT, R.J. (1996). Identification of annually produced opaque bands in the shell of the freshwater mussel *Elliptio complanata* using the seasonal cycle of $\delta^{18}\text{O}$. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 372–379.
- VERMEIJ, G.J. (1993). *A Natural History of Shells*, Princeton University Press, Princeton.
- VILLELLA, R.F., SMITH, D.R. & LEMARIE, D.P. (2004). Estimating survival and recruitment in a freshwater mussels population using mark-recapture techniques. *American Midland Naturalist*, **151**, 114–133.
- WHITE, C.R. & SEYMOUR, R.S. (2004). Does basal metabolic rate contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological, and life-history variables. *Physiological and Biochemical Zoology*, **77**, 929–941.
- WILBERG, M.J., BENICE, J.R., EGGOLD, B.T., MAKASKAS, D. & CLAPP, D.F. (2005). *Yellow perch dynamics in southwestern Lake Michigan during 1986–2002*. *North American Journal of Fisheries Management*, **25**, 1130–1152.
- WILLIAMS, J.D., BOGAN, A.E. & GARNER, J.T. (2008). *Freshwater mussels of Alabama & the Mobile Basin in Georgia, Mississippi & Tennessee*. University of Alabama Press, Tuscaloosa.
- WINEMILLER, K.O. & ROSE, K.A. (1992). Patterns of life-history diversification in North American fishes: implications for population and regulation. *Canadian Journal of Fisheries and Aquatic Science*, **49**, 2196–2218.
- ZIUGANOV, V., SAN MIGUEL, E., NEVES, R.J., LONGA, A., FERNÁNDEZ, C., AMARO, R., BELETSKY, V., POPOVITCH, E., KALIUZHIN, S. & JOHNSON, T. (2000). Life span variation of the freshwater pearl shell: a model species for testing longevity mechanisms in animals. *Ambio*, **29**, 102–105.