Growth Curves of Four Species of Commercially Valuable Freshwater Mussels (Bivalvia: Unionidae) in Arkansas

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Abstract

North American freshwater mussels (Bivalvia: Unionidae) have been exploited commercially for over 100 years and have been regulated using shell size limits and/or harvest seasons. Presently, freshwater mussels are considered a threatened faunal group in North America due to the large numbers of endangered, threatened or special concern species. Therefore, management of this fauna should emphasize their long-term sustainability. The objectives of this study were 1) to construct von Bertalanffy growth curves for selected "commercially-most-valuable" species, *Fusconaia ebena, Megalonaias nervosa, Amblema plicata* and *Quadrula quadrula*, from five rivers and two reservoirs, 2) to compare species-specific von Bertalanffy growth curves from different rivers and reservoirs, and 3) to provide information on size at onset of sexual maturity in *F. ebena* and *A. plicata*. Von Bertalanffy growth curves of four commercially valuable Ambleminae species were used in this study to compare drainage-specific growth. Growth curves for all four species investigated were significantly different between pairs of drainages. Approximate size at onset of sexual maturity was determined for Arkansas *F. ebena* and *A. plicata*. Von Bertalanffy growth curves, coupled with life history and population dynamics information, could be useful in assessing and determining national/state harvest sizes and/or drainage specific harvest sizes once annual growth line formation is confirmed.

Introduction

North American freshwater mussels (Bivalvia: Unionidae) have been exploited through commercial harvest for the past 125 years. Between the late 1800s and early 1900s, North American harvesters sold tons of thick-shelled unionid species to the button industry (Coker et al., 1921). After the shell button industry was all but eliminated by the advent of plastics in the 1940s, a second wave of North American harvesting began in the 1960s. As recently as the mid 1990's, thousands of tons of shells per year were converted into spheres for transplant into oysters, driving the multi-million dollar cultured pearl industry (Williams et al.,

1993). Commercial harvest today and the recent past is conducted by brailing and diving. In brailing, dragging treble hooks across the open gape of the unionid stimulates the closure of the valves onto the treble hook. Individuals are then lifted to the surface for processing. Brailing is a harvest method that extracts freshwater bivalves burrowed in the substrate, regardless of size or species. A more conservative and efficient method is hand collection via Hookah diving techniques. Divers descend to the bottom of the lake, reservoir or river and selectively harvest legal size specimens of target species. Because approximately 72% of the 297 native North American freshwater mussels (Bivalvia: Unionidae and Margaritiferidae) are endangered, threatened or of spe-

cial concern (Williams et al., 1993), much management attention has become focused on developing harvest regulations and management goals that ensure the long-term sustainability of this faunal group and fishery.

Historically, several methods have been employed to limit the harvest of unionids. Early regulations set by government agencies lacked size limits or employed size limits that did not adequately protect the resource (Thiel and Fritz, 1993). Since these early regulations, states such as Ohio and Mississippi have completely closed their commercial fisheries of unionids, while other states have set limited harvest seasons and size limits (Thiel and Fritz, 1993). Currently, efforts are being made to standardize size limits of harvestable species in the United States (J. Garner, Alabama Game and Fish, personal communication). However, development of effective size limits is hampered by the lack of life history and population information about commercially harvested species. Governmental agencies (e.g. Arkansas Game and Fish Commission; Wisconsin Department of Natural Resources (DNR), Kansas DNR, United States Fish and Wildlife Service) have established freshwater mussel refuges, thereby protecting some habitats from harvesting and physical habitat degradation.

If size limits are to be used for regulating harvest and assuring sustainability, basin-specific growth curves for individual species need to be generated and compared before appropriate standardized size limits are implemented. Growth curves are generated using length (or some measure of size) at age for different aged organisms. In a comparison of four shell-aging techniques (ashing, thin sectioning, acetate peels and counting external annuli), thin sectioning was found to be the best method of accurate age determination (Neves and Moyer, 1988). Using this technique, age is determined by counting the internal annuli of shells sectioned to a thickness of 350 microns (Neves and Moyer, 1988). While single annuli have been used to represent one year of growth, recent reports suggest that any non-annual external annuli (i.e. less than one annulus per year) used with growth curves can greatly over estimate growth and under estimate age of unionids (Downing et al., 1992; Downing and Downing, 1993; Kesler and Downing, 1997).

Although internal growth lines may not always coincide with absolute measures of periodicity (regarding number of days), growth curves could be used to compare shell growth within drainage basins experiencing similar energetic processes. For example, thin-sectioning techniques were used to age *Elliptio complanata* from different substrata in a Rhode Island lake. Von Bertalanffy growth curves generated from those measurements showed that growth rate was more related to substratum types than calendar days for *E. complanata* (Kesler and Bailey, 1993). Other authors have also shown that mussels grow at different rates under differ-

ent environmental conditions (e.g. Negus, 1966; Stansbery, 1967; Bailey and Green, 1988; Hinch et al., 1989). Therefore, it seems that growth curves generated from thin-sectioning techniques and von Bertalanffy growth equations can be used to investigate basin-specific growth and are reflections of the organisms' interactions with the environment via nutrient and energy expenditures.

This study is a component of a larger project that surveyed the commercial freshwater mussel beds in 10 rivers and three reservoirs in Arkansas between 1991 and 1997. The objectives of this study were 1) to construct von Bertalanffy growth curves for selected "commercially-most-valuable" species, (i.e. *Fusconaia ebena, Megalonaias nervosa, Amblema plicata* and *Quadrula quadrula*), from each of the five rivers or two reservoirs investigated, 2) to compare species-specific von Bertalanffy growth curves from pairs of rivers and a pair of reservoirs, and 3) to provide information about size at onset of sexual maturity in *Fusconaia ebena* and *Amblema plicata*.

Methods and Materials

Study Areas.--The White River originates in northwest Arkansas and flows for approximately 1,210 km. It drains approximately 75,520 km^2 of the Ozark Plateau and Mississippi Alluvial Plain physiographic provinces before entering the Arkansas River 16 km above its confluence with the Mississippi River. The White River was surveyed for freshwater mussel aggregations from the mouth to 416 km upstream (Fig. 1; Christian, 1995). The lower 240 km of the Black River that was surveyed in Arkansas is located in the Mississippi Alluvial Plain and drains approximately 22,165 km^2 before joining the White River (Rust, 1993). The Cache River, another tributary of the White River, is 229 km in length and drains 5,227 km^2 of the Mississippi Alluvial Plain. Only the lower 68 km of the Cache River, which is the portion of the river that is commercially harvested for unionids, was surveyed (Christian, 1995). The St. Francis River is a tributary of the Mississippi River and in Arkansas drains 13,466 km^2 within the Mississippi Alluvial Plain. The lower 200 km of the St. Francis River were surveyed (Posey, 1997). The Ouachita River, a tributary of the Red River, drains 17,411 km^2 of the Gulf Coastal Plain physiographic province. The lower 248 km of the Ouachita was surveyed (Posey, 1997). Ozark and Dardanelle lakes, formed by lock and dam units of the Kerr-McClellan Arkansas River Navigation System, were surveyed in 1996. They have surface areas of 4,291.5 and 12,591 ha, respectively (Davidson, 1997). All study drainages are located in the lower Mississippi River Basin.

Experimental Design.--The commercially-most-valuable unionid species, based on Arkansas Game and Fish harvest records, was collected from each river during sever-

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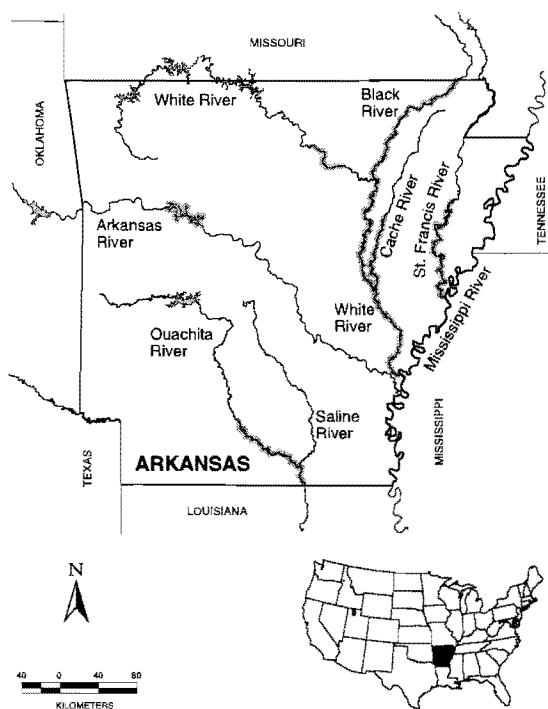
Fig. 1. Study areas (shaded) in the White, Black, Cache, St. Francis and Ouachita rivers and Ozark Lake and Lake Dardanelle (Arkansas River), Arkansas.

al field seasons plus an additional population of *Amblema plicata* was collected from the White River to compare with the Ouachita River *A. plicata* (Table 1). These four species of Unionidae, *Fusconaia ebena, Megalonaias nervosa, A. plicata* and *Quadrula quadrula*, belong to the subfamily Ambleminae, whose species are characterized by large thick shells, a lack of sexual dimorphism, hook-less glochidia, and

a relatively long life span. These four species are generally widely distributed in the Mississippi River Basin (Oesch, 1984; Cummings and Mayer, 1992; Vidrine, 1993).

Fusconaia ebena broods from April to September (Gordon and Layzer, 1989), has five known fish hosts from the families Centrarchidae (4) and Clupeidae (1) and reaches a maximum depth (dorsal to ventral margin of the shell) of 10.2 cm (Cummings and Mayer, 1992). *Megalonaias nervosa* is one of the largest unionid species reaching a depth of 27.9 cm (Cummings and Mayer, 1992), and there are 18 known fish hosts from the families Centrarchidae (5), Ictaluridae (5), Clupeidae (2), Amiidae (1), Anguillidae (1), Catostomidae (1), Percichthyidae (1), Percidae (1) and Sciaenidae (1). *Megalonaias nervosa* has been reported as both a short term and long term (bradytactic) brooder (Gordon and Layzer, 1989) with embryos or glochidia reported in the marsupium from September through February and also in April and May. *Amblema plicata* reaches a maximum depth of 17.8 cm (Cummings and Mayer, 1992), is a short-term (tachytictic) brooder from May to August, and 13 fish species representing the families Centrarchidae (7), Percidae (2), Esocidae (1), Ictaluridae (1), Lepisosteidae (1) and Percichthyidae (1) are known as hosts to the larval mussel stages (Gordon and Layzer, 1989; Watters, 1994). *Quadrula quadrula* reaches a maximum depth of 14 cm (Couch, 1997), broods young from April through August (Gordon and Layzer, 1989), and only one fish species, the ictalurid *Pylodictus olivaris*, has been reported as a fish host (Oesch, 1984).

Each species was collected from a variety of substrate types, water depths, and locations while diving within each water body. Specimens were fixed in a 10% formalin solution for transport to the laboratory. All soft tissue of each individual was removed in the laboratory, and shells were numbered and allowed to dry. Shell length (anterior to posterior margin), shell depth (dorsal to ventral margin) and shell width (right to left umbonal region) were measured in

Table 1. Commercially-most-valuable species collected.

Species	Location	Collection dates	Number collected
Fusconaia ebena	White River	July - October 1991-1994	52
	Black River	May - October 1991-1992	39
Megalonaias nervosa	Cache River	May - July 1993	38
	St. Francis River	May - July 1994	48
Amblema plicata	White River	June 1997	22
	Ouachita River	May - October 1993-1995	50
Quadrula quadrula	Ozark Lake	May - September 1996	49
	Lake Dardanelle	May - September 1996	49

mm using dial calipers. Age was estimated for each individual using internal growth lines visible following the thin-sectioning of shells after the methods of Neves and Moyer (1988). Growth curves were estimated for each population using the von Bertalanffy growth equation (Ricker, 1975), defined as:

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

where l_t is the length at time (t, years) of capture, $L \infty$ is the asymptotic length, k is the growth constant and t_0 is length at time zero. In addition to calculating the von Bertalanffy growth equation for length, equations were also developed for depth and width measurements. All four species investigated in this study are regulated by size limits based on shell depth, therefore growth estimates and models were developed for shell depth in order to relate to the harvest size parameter. Fitted von Bertalanffy growth curves were created in SAS using the Gauss-Newton method of non-linear least squares iterative phase (SAS INSTITUTE, 1988). For each size prediction of an age, 95% confidence intervals (CI) were estimated. To test whether there were significant differences in growth curves between populations, calculated F values were determined using methods reported in Chen et al. (1992) and compared with critical F with the appropriate degrees of freedom of the numerator and denominator. This method compares the summed residual sum of squares (RSS) error of individual growth models to the RSS error of a pooled data model. A significant difference between estimated parameters (i.e., L, k or t_0) of each

von Bertalanffy model was based on non-overlapping ranges of the 95% CI.

Sexual maturity (i.e. production of gametes) was determined for two species, *Fusconaia ebena* and *Amblema plicata*, for which published data on sexual maturity are minimal to non- existent. No determination of *Megalonaias nervosa* sexual status was attempted because information was available on *M. nervosa* from Pool 10 in the upper Mississippi River which reported this species to become reproductively mature by age eight (Woody and Holland-Bartels, 1993). Individuals used for sexual maturity analysis were collected in the summer of 1997 from the White River between Newport and Augusta, AR and collected separately from individuals used for shell thin-section analysis. No determination of *Quadrula quadrula* sexual status was attempted because no individuals were collected for analysis in 1997. Size measurements were recorded in the same fashion as reported previously. Sexual maturity was determined by removing gonadal tissues using a biopsy needle, smearing gonadal tissue on a standard microscope slide, and determining the presence of gametes in each individual using a compound microscope under 10x, 100x and 400x magnification.

Results

Growth parameters for depth, length and width measurements for the Black River and White River *Fusconaia*
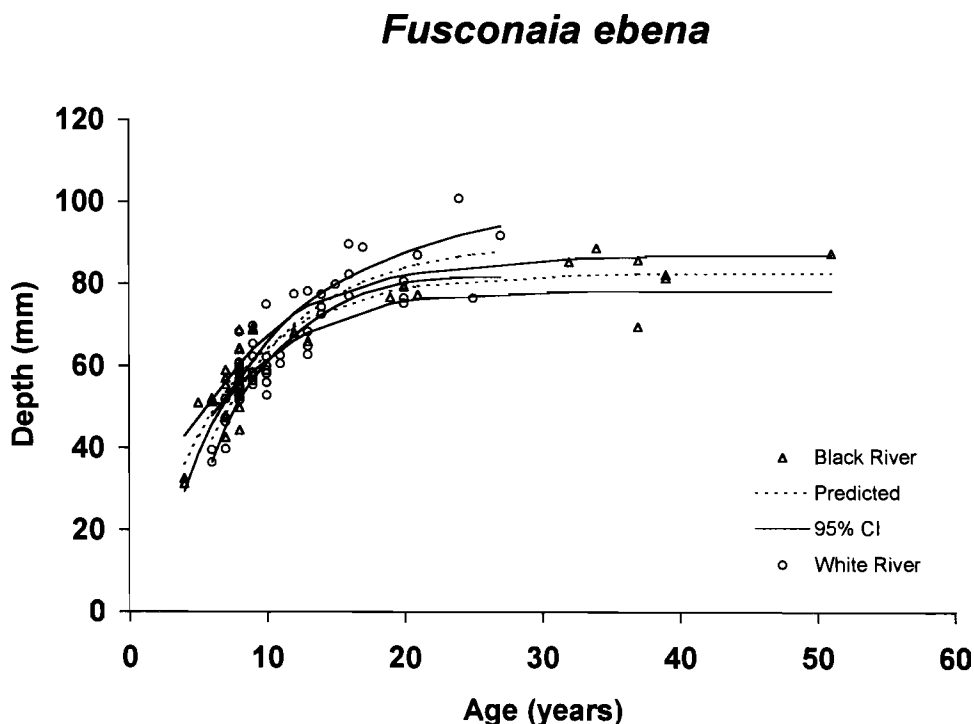

Fig. 2. Estimated von Bertalanffy growth curve with 95% confidence intervals and observed age vs. depth of *Fusconaia ebena* of the Black and White rivers, Arkansas.

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ebena are reported in Table 2. The fitted von Bertalanffy growth curves for the depth measurement of *F. ebena* from the Black and White rivers are illustrated in Fig. 2 and were found to be significantly different based on a comparison of pooled versus summed individual RSS models ($P < 0.001$, Table 3). Sexual maturity, or first sign of gametes, in *F. ebena* was determined to occur at a depth of at least 46.7 mm in individuals ranging in depth from 46.7 to 81.0 mm (n = 26),

however, production of gametes probably occurs at a smaller size than our size range.

Fitted growth curves for *Megalonaias nervosa* from the Cache River and St. Francis River are illustrated in Fig. 3. There was a significant difference between the Cache River and St. Francis River growth curves for the depth measurement based on a comparison of pooled versus summed individual RSS models ($P < 0.001$, Table 3). Table 2 sum-

Table 2. Estimated von Bertalanffy growth parameters, asymptotic length (L∞), growth constant (k) and length at time zero (t_0), for selected species and drainages with 95% confidence interval (CI) in parentheses. Superscripted letters a-d indicate significant differences in growth parameters based on non-overlapping 95% CI.

| Species	Parameter	Location	L	k	t_0
Fusconaia ebena					
	Depth	Black	82.61 ± (4.42)	0.16± (0.06)	0.35 ± (1.94)
		White	90.30 ± (9.46)	0.14± (0.06)	1.62 ± (2.30)
	Length	Black	102.19 ± (5.98)	0.14± (0.06)	0.41 ± (2.0)
		White	115.91 ± (13.48)	0.13± (0.06)	2.09 ± (1.88)
	Width	Black	57.88 ± (3.22)	0.18± (0.06)	0.54 ± (1.98)
		White	61.30 ± (7.16)	0.16± (0.10)	1.35 ± (3.26)
Megalonaias nervosa					
	Depth	Cache	131.06 ± (14.36)	0.06± (0.02)	0.16 ± (1.52)
		St. Francis	144.83 ± (45.10)	0.03± (0.04)	-24.50 ± (25.20)
	Length	Cache	239.22 ± (43.92)	0.08± (0.02)	-1.07 ± (2.04)[a]
		St. Francis	217.79 ± (42.52)	0.04± (0.04)	-14.33 ± (11.96)[a]
	Width	Cache	184.73 ± (224.10)	0.01± (0.02)	-4.98 ± (5.78)
		St. Francis	70.62 ± (4.32)	0.07± (0.06)	-6.16 ± (9.10)
Amblema plicata					
	Depth	White	100.20 ± (25.86)[b]	0.11± (0.14)	1.01 ± (8.18)
		Ouachita	61.69 ± (3.96)[b]	0.17± (0.06)	-0.03 ± (1.34)
	Length	White	137.96 ± (42.10)[c]	0.09± (0.12)	0.83 ± (8.04)
		Ouachita	87.02 ± (7.80)[c]	0.13± (0.04)	-0.34 ± (1.50)
	Width	White	57.70 ± (5.68)[d]	0.19± (0.16)	3.19 ± (4.84)
		Ouachita	39.37 ± (2.90)[d]	0.17± (0.8)	-0.51 ± (1.88)
Quadrula quadrula					
	Depth	Dardanelle	73.14 ± (4.84)	0.14± (0.40)	0.10 ± (0.86)
		Ozark	8.08 ± (31.28)	0.09± (0.06)	0.01 ± (1.64)
	Length	Dardanelle	99.36 ± (11.32)	0.09± (0.03)	-0.88 ± (0.58)
		Ozark	19.96 ± (36.90)	0.10± (0.08)	-0.03 ± (0.85)
	Width	Dardanelle	49.16 ± (3.66)	0.13± (0.02)	0.01 ± (0.94)
		Ozark	60.07 ± (14.88)	0.11± (0.08)	0.08 ± (0.77)

Megalonaias nervosa
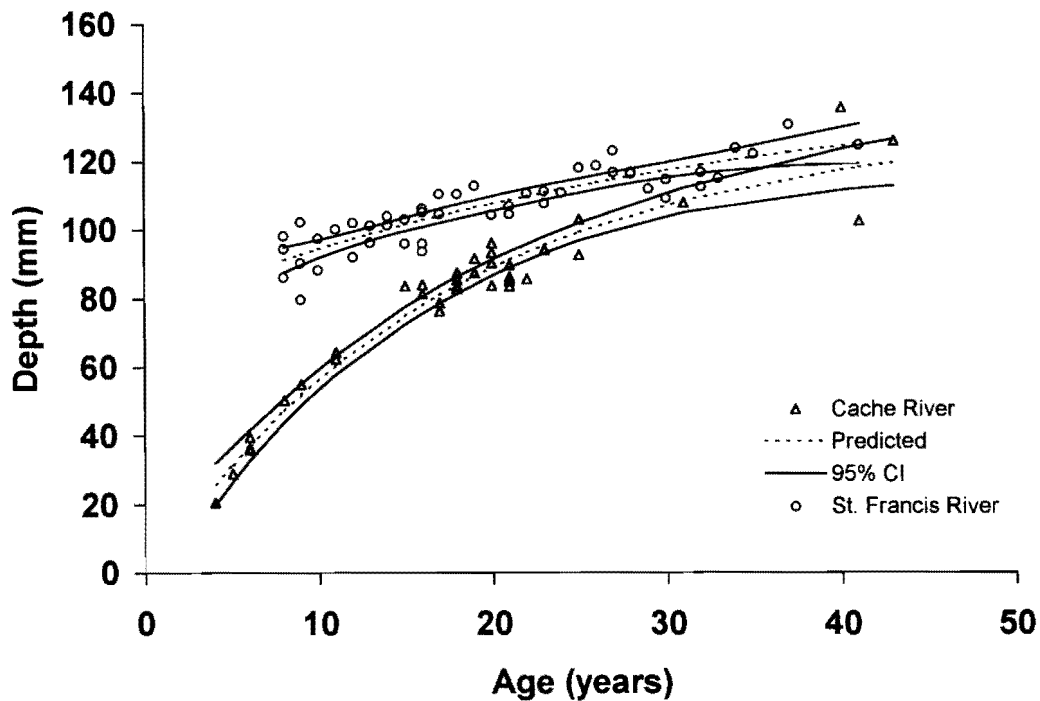
Fig. 3. Estimated von Bertalanffy growth curve with 95% confidence intervals and observed age vs. depth of *Megalonaias nervosa* of the Cache and St. Francis rivers, Arkansas.

marizes growth parameters for all size measurements.

Amblema plicata depth measurement growth curves for the Ouachita River and White River are shown in Fig. 4 and were found to be significantly different based on a comparison of pooled versus summed individual RSS models (P <0.001, Table 3). Growth parameters for all size measurements are summarized for this species and were found to be significantly different in the L growth parameter (asymptotic depth, length and width) based on non-overlapping 95% confidence intervals (Table 2). In *A. plicata* from the White

River, gametes were first observed at 21.9 mm in depth from individuals (n = 25) ranging from 16.4 to 41.3 mm.

Growth curves for the depth measurement of *Quadrula quadrula* from Ozark Lake and Lake Dardanelle are illustrated in Fig. 5 and were found to be significantly different based on a comparison of pooled versus summed individual RSS models (P <0.001, Table 3). *Quadrula quadrula* size measurement growth parameters for Ozark Lake and Lake Dardanelle are reported in Table 2.

Table 3. Species comparisons of growth modeled by von Bertalanffy growth formula by means of residual sum of squares (RSS) for pooled data (RSSp) and summed data (RSSs) including statistical significance.

Species	RSSp	DF	RSSs	DF	F	Pr>F
Fusconaia ebena	3738.20	88	3317.56	85	67.44	<0.0001
Megalonaias nervosa	16434.87	83	2446.89	80	510.66	<0.0001
Amblema plicata	4374.40	95	3290.34	92	91.64	<0.0001
Quadrula quadrula	7215.25	70	1940.77	67	226.75	<0.0001

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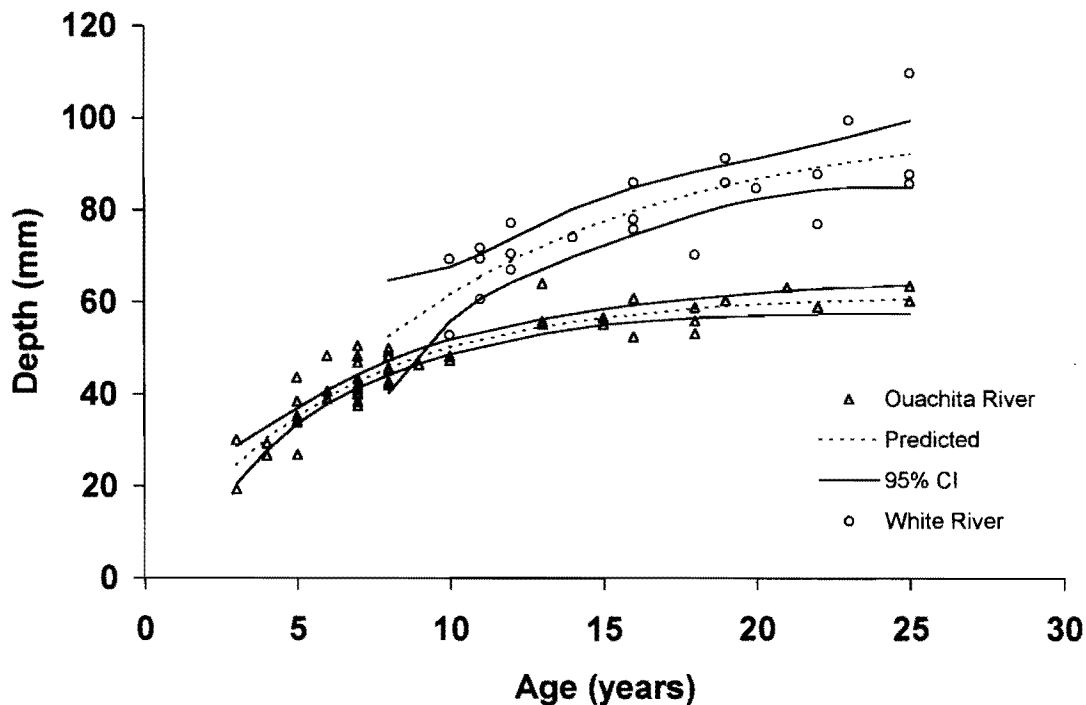
Fig. 4. Estimated von Bertalanffy growth curve with 95% confidence intervals and observed age vs. depth of *Amblema plicata* of the Ouachita and White rivers, Arkansas Predicted and 95% CI lines illustrated.

Discussion

The error of the pooled *Fusconaia ebena* models was greater than the individual summed models for depth indicating that the individual models for each river best explain the data. *Fusconaia ebena* from the Black and White rivers had significantly different growth (Fig. 2) even though individuals were taken from portions of their respective rivers found in the same Mississippi Alluvial Plain physiographic province. Whereas many of the mussel bed substrata were at least qualitatively similar, either soft-to-hard clay or gravel substrata (Rust, 1993; Christian, 1995), it is likely that some abiotic and/or biotic factors differed in the rivers. For example, the White River flows approximately 800 km in the Ozark Plateau physiographic province upstream of the study area and has different limnological parameters, such as calcium concentrations, than the Black River which is located mainly in the Mississippi Alluvial Plain. In addition, temperature differences due to hypolimnetic release dams on the White River (Miller et al., 1987), may also influence growth which may explain the slight differences in the growth rates (k) between White River and Black River models.

Megalonaias nervosa individuals were also collected from rivers that are located in the same physiographic province, the Mississippi Alluvial Plain, even though the headwaters of the St. Francis originate in the Missouri Ozarks. Again, abiotic and biotic factors are assumed to be similar. For example, substrates of defined mussel beds were qualitatively similar between the Cache and St. Francis rivers with mostly soft-to-hard clay to silty substrates mixed with sand (Christian, 1995; Posey, 1997). Nevertheless, the pooled RSS was much greater than the summed individual models suggesting differences in the models. One possible explanation for differences in the growth models may be the lack of small individuals collected from the St. Francis River (Figure 3). Asymptotic size seems similar in both rivers as does growth rate, but size at age zero is quite different. Lack of small *M. nervosa* individuals in the St. Francis River model may have influenced this parameter.

The pooled *Amblema plicata* model reflected more variance than the summed individual models suggesting differences between the individual models (Fig. 4, Table 3). The non-overlapping 95% confidence intervals in asymptotic (L) length, depth and width between the Ouachita River and White River suggest that some species of freshwater mus-
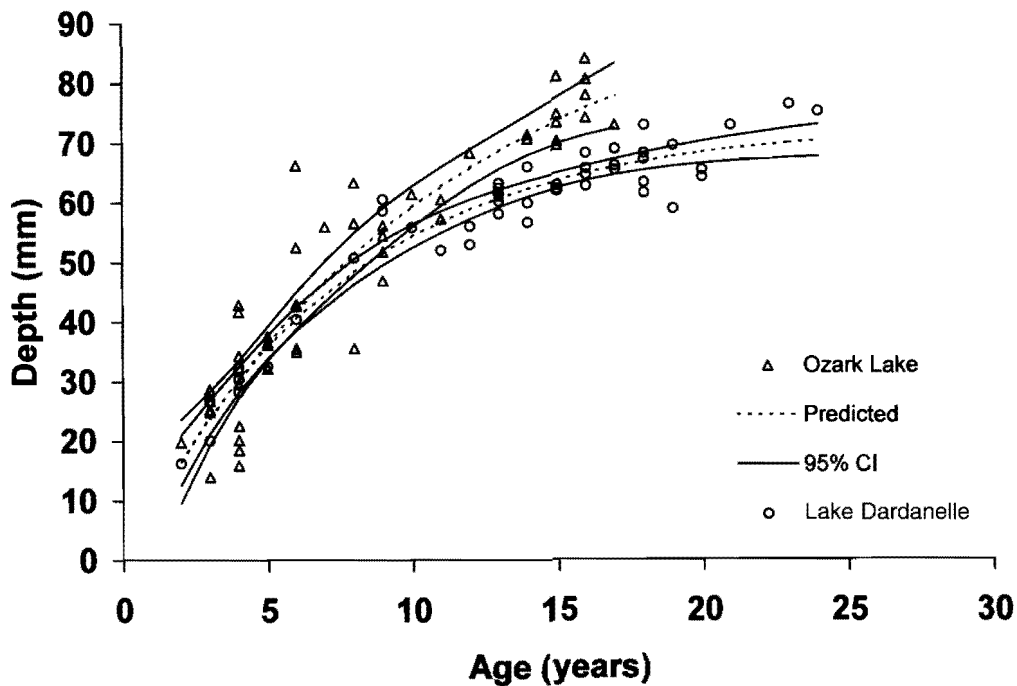
Quadrula quadrula

Fig. 5. Estimated von Bertalanffy growth curve with 95% confidence intervals and observed age vs. depth of *Quadrula quadrula* of the Ozark Lake and Lake Dardanelle, Arkansas.

sels, including *A. plicata*, in the Ouachita mid-order stream reaches tend to be smaller in overall size than in other streams in Arkansas (Fig. 4; WRP and JLH, pers. observ.). Within our survey sites, the Ouachita River basin substrate has a greater component of gravel compared to the dominant clay/sand substrates of the lower White River (Christian, 1995; Posey, 1997). Bailey and Green (1988) found that mussels in areas of high turbulence and sandy substrate had thicker shells than those from less turbulent areas. In addition, mussels from more turbulent areas grew at a faster rate. Alternatively, Kesler and Bailey (1993) reported that *Elliptio complanata* grew at a faster rate in the silt substratum. However, they speculated that individuals in the silt substratum may have had a richer food supply, which increased their growth rate, or that the individuals in the sand substratum were located in extreme turbulence, reducing their growth. Ambient water quality conditions can also contribute to the above mentioned basin habitat factors to differentiate growth. Low water hardness of 20 mg $CaCO_3$/L as in the Ouachita River would be sufficient to reduce shell size when compared to individuals from the White River with calcium hardness of 140 mg/L (Posey, 1997).

Growth rate (k) of *Amblema plicata* was not significantly different, based on overlapping 95% confidence intervals, between the Ouachita River and White River, which would not have been predicted because asymptotic growth is different between the two populations. This suggests that while rates are similar, there comes a point at which growth decreases earlier in Ouachita River than the White River. Growth senescence as indicated by a flattening of the growth curve might suggest the occurrence of a life history trade-off. Use of energy and mineral resources for reproduction may be a trade-off in locations where calcium or other resources are limited (e.g., Ouachita River).

Similarities in growth parameters of *Quadrula quadrula* populations from the two reservoirs were expected due to the similar abiotic and biotic conditions of the reservoirs; however, summed individual reservoir models were less variable than a pooled model again indicating that the individual models for each reservoir best explained the data (Fig. 5, Table 3). Substrata of mussel beds were similar, consisting of silt (Davidson, 1997).

While we acknowledge the controversy as to whether an annulus is deposited each year, we still believe that thin-sectioning combined with von Bertalanffy growth curves

can be used effectively to compare growth between populations within a region. It is understood that these models can underestimate age and overestimate growth (Kesler and Downing, 1997), but within the context of our comparisons, we assumed these processes to be similar between the populations. In order to use these models to estimate age and growth of populations, verification of annuli is needed through experimentation over at least three years using methods similar to those of Kesler and Downing (1997). While assuming that ecological processes, (e.g. those that influence energy expenditures and allocations in mussels) of rivers and/or reservoirs within a region are similar, we have shown that differences in growth are occurring between mussels from different rivers and reservoirs. These growth differences could have management implications, especially when considering size/age at legal harvest. Therefore we have shown that basin specific growth in these species needs to be considered when managing the commercial component of this imperiled fauna.

The thin-section aging and von Bertalanffy growth curve techniques utilized in our study could contribute to components of a multi-phase management scheme consisting of 1) employment of standardized sampling methods by managers to consistently estimate population size and monitor population dynamics (e.g. dominant cohorts), 2) investigation of life history characteristics such as drainage-specific growth, sexual dimorphism, age at sexual maturity, brood size, brooding strategies (short-term versus long-term) and characterization of size class survivorship for individual species, 3) establishment and maintenance of regional refuge areas along the stream system, and 4) reporting of specific harvest locations and numbers taken by commercial harvesters at shell buying sites.

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