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Abstract.—The life history and population demography of the endangered birdwing pearlymussel (*Lemiox rimosus*) were studied in the Clinch and Duck rivers, Tennessee. Reproducing populations of *L. rimosus* now occur only in the Clinch, Duck and Powell rivers, as the species is considered extirpated from the remaining portions of its range in the Tennessee River drainage. Females are long-term winter brooders, typically gravid from Oct. to May. Glochidia are contained in the outer gills and are released in association with a mantle-lure that resembles a small freshwater snail. Estimated fecundity, based on 8 gravid females collected from the Clinch and Duck rivers, ranged from 4132 to 58,700 glochidia/mussel. Seven fish species were tested for suitability as hosts for glochidia, and five darter species were confirmed through induced infestations: *Etheostoma blennioides*, *E. camurum*, *E. rufilineatum*, *E. simoterum* and *E. zonale*. Ages of *L. rimosus* shells were determined by thin-sectioning and ranged from 3 to 15 y in both rivers. Shell growth was higher and maximum size greater in males than females in both rivers. Shell growth was greatest in the Duck River. Densities of *L. rimosus* in the Clinch River were maintained at seemingly stable but low levels ranging from 0.07 to 0.27 m^{-2} from 2004–2007, and in the Duck River at similar but higher levels ranging from 0.6 to 1.0 m^{-2} from 2004–2006. In the latter river, abundance has increased since 1988, likely due to improved minimum flows and dissolved oxygen levels in water releases from a reservoir upstream.

Introduction

The birdwing pearlymussel (*Lemiox rimosus*) typically inhabits gravel shoals of medium-to-large rivers of the Cumberland Plateau and Southern Appalachian Mountains (Ortmann, 1918). The species was first described by Rafinesque (1831) from the Cumberland River; however, it was never again reported from this river system (Wilson and Clark, 1914; USFWS, 1984). Hence, the locality information for the original collection record may be erroneous.

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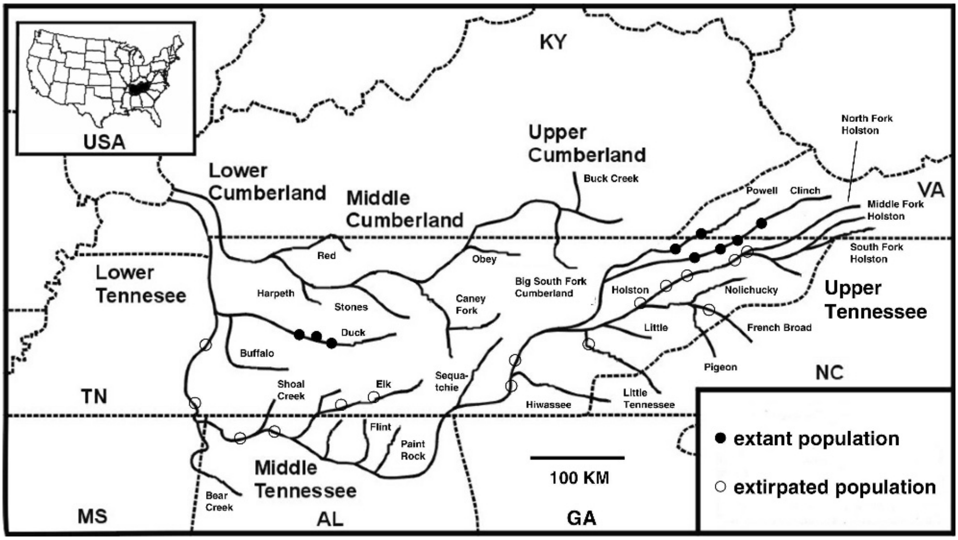

FIG. 1.—Historic and current distribution of *Lemiox rimosus* in the Tennessee River drainage

Historically, this species was widespread throughout the Tennessee River drainage (Parmalee and Bogan, 1998) (Fig. 1). It once occurred in this drainage from its major headwater tributary streams (*e.g.*, Powell, Clinch, Holston and French Broad rivers), downstream to Muscle Shoals in northern Alabama, and in the Duck River, Tennessee (TN) (Ortmann, 1918, 1924, 1925; USFWS, 1984). Although the species was once widespread throughout the drainage, it was never considered abundant at any location (Ortmann, 1918). Reproducing populations of *L. rimosus* now are restricted to the Clinch and Powell rivers in Virginia (VA) and TN, and in the Duck River, which is considered to have the largest population (USFWS, 1984; Parmalee and Bogan, 1998). Currently, the species occupies <10% of its historic range, occurring in only ~170 river kilometers (rkm) in the Clinch River, ~84 rkm in the Powell River and ~60 rkm in the Duck River (USFWS, 1984). These remaining populations are disjunct, and range reductions and population declines may still be occurring even within the Clinch and Powell rivers (Ahlstedt and Jenkinson, 1987; Ahlstedt, 1991; Ahlstedt and Tuberville, 1997; Ahlstedt *et al.*, 2005). Dams, channel dredging, sand and gravel mining, coal mining, sewage wastes and agricultural run-off have caused or have likely contributed to declines in populations throughout its range. Because of severe population declines during the twentieth century, *L. rimosus* was listed as endangered by the U.S. Fish and Wildlife Service in 1976 (Federal Register 41:24062–24067). The objective of our study was to provide needed biological data specified in the federal recovery plan for this species (USFWS, 1984), and to gather information on current distribution, life history and demography to aid in recovery.

METHODS

Collection and examination of gravid female mussels.—Gravid females of *Lemiox rimosus* were obtained by snorkeling and examined for gravidity by opening the valves slowly by hand to look for swollen gills containing glochidia. Female mussels were typically collected in fall and spring in the Clinch and Duck rivers. Female mussels were held in temperature-controlled, water-recirculating artificial streams with gravel-filled bottoms at the Freshwater Mollusk Conservation Center at Virginia Polytechnic Institute and State University, Blacksburg, to study life history. Depending on when mussels were collected, water temperatures in the artificial streams were set at 15 to 20 C to mimic ambient river temperatures.

The number of glochidia (fecundity) from 2 females collected in the Clinch River and 6 females collected in the Duck River was estimated by flushing glochidia from the outer gills of each female with a hypodermic needle filled with water. All glochidia were counted for smaller females using a dissecting microscope to determine the number of glochidia/female to estimate fecundity. However, for the larger females, sub-samples of glochidia were counted from 1 ml aliquots (n = 3), and fecundity assessed volumetrically. Maturity of the glochidia was tested by exposing a small subset (~100) to a dilute salt solution (Zale and Neves, 1982). Glochidia were deemed mature when >20% exhibited rapid, sometimes multiple, snapping responses when exposed to the NaCl solution. Dimensions (length = anterior to posterior, height = dorsal to ventral) of 20 glochidia from each female mussel were measured using an ocular micrometer.

Live female mussels were held in temperature-controlled (21–22 C) artificial streams for photo-documentation. This laboratory set-up allowed females to display their mantle-lure and for behavioral observations of lure movements that were recorded under controlled conditions. All behavioral observations were made during daytime hours. Photographs of the mantle-lure were taken using a Nikonos V underwater camera with a 35 mm lens and Kodak 200 Ektachrome film.

Fish hosts.—Based on preliminary studies conducted by Hill (1986) and Watson (1999), we focused primarily on testing various darter species and one species of sculpin as potential hosts. Most of the fish were collected from the upper North Fork Holston River, ~1 km above Saltville, Smyth County, VA. Black sculpins (*Cottus baileyi*) were collected from the Middle Fork Holston River at Atkins, Smyth County, VA. Gilt darters (*Percina evides*) were collected from the Powell River, Lee County, VA, at the State Route 833 bridge where *Lemiox rimosus* was rare. All other fish collection sites had few mussels and no birdwing pearlymussels. Fishes were collected using low voltage (200–250 V) electroshocking to ensure survival. Common and scientific names follow Robins *et al.* (1991) for fishes and Turgeon *et al.* (1998) for mussels.

Methods for infesting fish with mussel glochidia generally followed Zale and Neves (1982). A plastic container 29 × 19 × 12 cm deep was used to hold fish during infestation. Fish of various species were held simultaneously in ~0.5 L of water, and glochidia from 1–3 females were added to the container. The water in the container was constantly agitated by using 2 air stones positioned on opposite sides for ~1 h. After infestation, fish were separated by species and placed in 38-L aquaria without substrate. Fish species were held separately at low densities (6–8/aquaria) in a water-recirculating fish-holding system. The bottoms of the aquaria were siphoned every 2 to 3 d until juvenile mussels were first collected, and every 1 to 2 d thereafter. Juveniles were counted and placed in a culture dish with sediment and algae for rearing. Collection of mobile juveniles confirmed that the glochidia had transformed on the fish species, and that species was a potential natural host of *Lemiox rimosus*.

Age and growth.—Fresh-dead shells of *Lemiox rimosus* were collected from various locations in the Clinch and Duck rivers, TN between 1998 and 2007. Shells of various lengths were collected to best represent the size-class structure of the population of each river. Thin-sections of shells were prepared following procedures described by Clark (1980) and Neves and Moyer (1988), using a Buehler Isomet low-speed saw unit with a diamond-impregnated blade (Buehler, Evanston, Illinois). Shells were cut from the center of the umbo to the ventral margin. Cut valves were glued (2-Ton Clear Epoxy, Illinois Tool Works, Devcon, Massachusetts) to petrographic microslides (27 × 46 mm), vacuum-sealed into a petrographic chuck, attached to the cutting arm of the saw and sectioned at a thickness of 280 μm (Neves and Moyer, 1988). Thin-sections of shells were examined under 40× magnification. Internal growth lines were considered true annuli if they were continuous from the umbo region to the outer surface of the shell. It was assumed, based on shell-aging in the rivers of southwest Virginia (Neves and Moyer, 1988), that one annulus was formed each year. Lengths for 1 and 3 y old individuals, and occasionally older age classes, were obtained by back-calculating length-at-age based on internal annuli of 5 older shells (Bruenderman and Neves, 1993) because shells <3 y old and >10 y old were difficult to collect from the river. Mean shell lengths and age for each sex were fitted to von Bertalanffy growth curves.

Population demography.—Several population demographic characteristics, such as density, abundance and age-class frequency, were estimated at sites in the Clinch and Duck rivers. In addition, a time series (1979–2004) of mussel density data was analyzed for the Clinch River at Kyles Ford, Hancock Co., TN (Ahlstedt *et al.*, 2005), and Duck River at Lillard's Mill, Marshall Co., TN (Ahlstedt, 1991; Ahlstedt *et al.*, 2004). These two sites are considered the best locations for the species in each river, respectively. The number of quadrat samples taken at Kyles Ford was n = 41 per sampling interval, and at Lillard's Mill n = 40 in 1979, n = 41 in 1988 and n = 20 in 2004. These data were collected by random 0.25 m^2 quadrat sampling in shoal areas that typically contained the highest mussel densities at the respective sites to facilitate long-term monitoring. Additional data from 2004–2007 were collected from both rivers by systematic, 0.25 m^2 quadrat sampling placed along transect lines evenly spaced throughout the entire shoal area [J. Jones, USFWS, unpublished data; B. Ostby, Virginia Polytechnic Institute and State University (VPISU), unpublished data; Adair, 2005]. Total area (m^2) of gravel shoals (mussel beds) was determined by multiplying mean river width, measured at 10 m intervals, by total length of each reach. Small, exposed gravel bars and islands not containing mussels but within the immediate shoal area were measured and removed from analysis. Site dimensions (length and width) were measured using a standard 100 m measuring tape. Upstream and downstream limits of the shoal were determined by visually inspecting for substrate composition (*e.g.*, an abrupt change from suitable gravel substrate to unsuitable bedrock or soft sediments), water depth, flow velocity and absence of mussels. All 0.25 m^2 quadrats were excavated to hardpan, or to approximately 20 cm in depth. Mussels were measured for length (nearest 0.1 mm) using digital calipers and replaced at their approximate position of collection. Population size at each site was estimated by multiplying mussel density (m^{-2}) by total site area.

Age-class frequency was determined by aging live mussels collected from 2004-2007 using predicted lengths-at-age as computed by a von Bertalanffy growth curve (VBGC) (von Bertalanffy, 1938). The VBGC is a modified logistic model written as:

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)}\right]$$

where L_∞ (L-infinity) is a theoretical maximum (asymptotic) length, k is a growth coefficient, t is time or age in years, t_0 is the time in years when length would theoretically be equal to zero, and e is the natural log exponent. The species is sexually dimorphic, so all age and growth analyses were conducted separately for males and females in both rivers.

FIG. 2.—Mantle display (~0.75 cm long) of *Lemiox rimosus* is indicated by white arrow. The display closely resembles a small snail, which is a known prey item of some of its fish hosts

Data analyses.—Descriptive statistical analyses of glochidia and shell lengths and mussel densities were conducted in MINITAB 14 Statistical Software (Minitab, Inc., State College, Pennsylvania). A one-way analysis of variance (ANOVA) was used to test whether dimensions of glochidia were significantly different among females. A repeated measures ANOVA was used to test whether mussel density among sample years was significantly different. Parameters of the VBGC were estimated using Fisheries Analyses and Simulation Tools software (FAST 2.0) (Auburn University, Alabama).

RESULTS

Release of glochidia and fecundity.—Glochidia of *L. rimosus* were contained only in the outer gills of females, and their ''tear-drop'' shape is typical of many lampsiline species (Hoggarth 1999). The average size (±95% CI) of a glochidium was 0.226 (±0.008) mm long and 0.254 (±0.009) mm high. No significant differences were observed among females in dimensions of their respective glochidia. Glochidia were released in association with a mantle-lure display that appears to mimic a small aquatic snail (Fig. 2). The mantle-lure has the color and whorl pattern of snails in the genus *Leptoxis.* In the laboratory, we observed the mantle-lures of numerous females (n = 6) moving in a subtle side-to-side motion that seemingly mimics the locomotion and feeding behavior of a snail. In the field, we observed females displaying the mantle-lure in the Clinch River, TN, in both fall and spring of the year. In the Clinch River, females were gravid from Oct. through May (Table 1). Fewer data were available to determine gravid periods for females in the Duck River, but collections made during this study and others indicated that gravidity likely occurs from Aug. through Jul. (Table 2). For example, gravid individuals were observed in Jun. and Jul. by Hill (1986), and

TABLE 1.—Reproductive condition of females of *Lemiox rimosus* collected from the Clinch River between 1997 and 2007

	Oct.–Nov.	Dec.–Jan.	Feb.–Mar.	Apr.–May	Jun.–Jul.	Aug.–Sept.
No. examined	9	1	3	25	6	1
No. gravid (%)	4 (44)	0 (0)	3 (100)	4 (16)	0 (0)	0 (0)

in late Aug. (B. Ostby, pers. obs., 2007). Fecundity of examined females ranged from 4132 to 58,700 glochidia/female (Table 2).

Fish hosts.—Five species of darters (Percidae) were identified as hosts from induced infestations of glochidia: greenside darter *Etheostoma blennioides*, bluebreast darter *E. camurum*, redline darter *E. rufilineatum*, snubnose darter *E. simoterum* and banded darter *E. zonale* (Table 3). Fish host usage and transformation success of glochidia were similar between the Clinch and Duck river populations. All of the identified fish hosts were native to the Tennessee River system (Etnier and Starnes, 1993), and sympatric with *Lemiox rimosus* in all or part of its range. Peak transformation of glochidia to juveniles was protracted (>50 d) for infestations conducted in fall vs. spring (Table 3). For example in fall of 1997, *E. blennioides* and *E. zonale* were infested together, and excystment of juveniles peaked at 72 d and finished at 122 d (Fig. 3).

Age and growth.—In the Clinch River, sample size of male shells was n = 31 and total sample size was n = 66, which includes back-calculated length-at-age measurements (Table 4). Sample size of female shells was n = 8 and total sample size n = 44. In the Duck River, sample size of male shells was n = 51 and total sample size was n = 86; sample size of female shells was n = 14 and total sample size was n = 57.

Based on aging of shells, the maximum age observed in either the Clinch or Duck river populations was 15 y for males and 11 y for females. The smallest gravid individuals observed in either population ranged from 28 to 32 mm, implying that most females were mature at 4 to 5 y. In the Clinch River, predicted shell growth for males averaged 3.8 mm/y through age 0–10 y and decreased to 1.9 mm/y thereafter; females averaged 4.4 mm/y through age 0–6 y and decreased to 0.6 mm/y thereafter (Fig. 4; Table 4). In the Duck River, shell growth for males averaged 4.7 mm/y through age 0–10 y and decreased to 0.6 mm/y thereafter; females averaged 5.1 mm/y through age 0–6 y and decreased to 0.5 mm/y thereafter. Higher growth in the Duck River also is reflected in VBGC parameter estimates of the growth coefficient k, which were 0.244 y^{-1} (males) and 0.402 y^{-1} (females), compared to 0.072 y^{-1} (males) and 0.309 y^{-1} (females) in the Clinch River (Fig. 4). Furthermore, a bias for higher k in females is noted, and population comparisons are only valid within sexes.

TABLE 2.—Shell lengths and fecundity estimates for gravid females of *Lemiox rimosus*

Date examined	River	Shell length (mm)	Glochidia/mussel
3 Nov. 1997	Clinch	38.0	6479
11 No. 1998	Clinch	35.2	4132
25 Oct. 2001	Duck	32.7	10,744
25 Oct. 2001	Duck	34.5	10,320
25 Oct. 2001	Duck	27.3	7066
5 May 2007	Duck	39.5	21,800
5 May 2007	Duck	42.3	13,530
5 May 2007	Duck	43.0	58,700

TABLE 3.—Results of induced infestations on potential fish hosts with glochidia of *Lemiox rimosus*. Days-to-transformation was the first day and last day when juveniles excysted from a fish host. The peak (in parentheses) was when most juveniles excysted. Temperature is the mean water temperature in the aquaria where fish were held. * = successful host species; ND = no data

Fish species	No. fish tested	No. fish alive	Time (d)	Juveniles recovered	Days to transformation	Temperature (°C)
Cottidae						
Cottus baileyi[c]	15	14	93	0	ND	20.0
Percidae						
**Etheostoma blennioides*[a]	5	3	128	255	31, (72), 122	20.0
**E. blennioides*[b]	6	5	100	31	64, (72–74), 90	18.0
**E. blennioides*[c]	12	3	93	107	47, (57–70), 90	20.0
**E. blennioides*[d]	29	4	34	82	22, (25), 33	21.0
**E. blenniodes*[f]	26	15	66	18	12, (42), 46	21.0
**E. blenniodes*[g]	4	4	50	50	12, (36), 50	22.0
**Etheostoma camurum*[f]	7	4	66	1	17	21.0
Etheostoma flabellare[g]	4	4	50	0	ND	22.0
**Etheostoma rufilineatum*[f]	20	12	66	20	12, (14–18), 19	21.0
**E. rufilineatum*[g]	18	12	50	1	50	22.0
**Etheostoma simoterum*[a]	18	2	100	19	47, (62–72), 82	20.0
**E. simoterum*[c]	20	17	50	70	31, (40–45), 48	20.0
**E. simoterum*[d]	20	8	34	227	22, (31–32), 34	21.0
**Etheostoma zonale*[a]	15	6	90	73	31, (67–72), 85	20.0
E. zonale[d]	20	3	34	4	22–28	21.0
Percina evides[e]	15	12	65	0	ND	21.0

[a] Fish were infested together for 1 h with glochidia from 2 gills of 1 mussel from the Clinch River, TN on 3 Nov. 1997

[b] Fish were infested together for 1 h with glochidia from 2 gills of 1 mussel from the Clinch River, TN on 11 Nov. 1998

[c] Fish were infested together for 1 h with glochidia from 6 gills of 3 mussels from the Duck River, TN on 26 Oct. 2001

[d] Fish were infested together for 1 h with glochidia from 4 gills of 2 mussels from the Clinch River, TN on 5 May 2002

[e] Fish were infested together for 30 min with glochidia from 4 gills of 2 mussels from the Clinch River, TN on 28 May 2004

[f] Fish were infested together for 40 min with glochidia from 6 gills of 3 mussels from the Duck River, TN on 4 May 2007

[g] Fish were infested together for 60 min with glochidia from 2 gills of 1 mussel from the Clinch River, TN on 24 Jun. 2007

Population demography.—In the Duck River, sample size of live individuals (n = 117) was greater and better represents the actual age-class structure of the population (Fig. 5). Similarly, younger and middle-aged individuals predominate and constitute >80% of the sample, demonstrating high levels of recent recruitment in the population. In the Duck River, the VBGC equations predict that older individuals (10–15 y) are evident and may include at least a few individuals >15 y, which can be seen in the age-frequency histogram. In contrast, total sample size of live individuals (n = 21) collected during quantitative sampling in the Clinch River from 2004–2007 was small; therefore, inferences about age-class structure are speculative (Fig. 5). However, the sample was composed mostly of sub-adults (1–3 y) and middle-aged (4–8 y) adults, suggesting that older individuals (>10 y) are

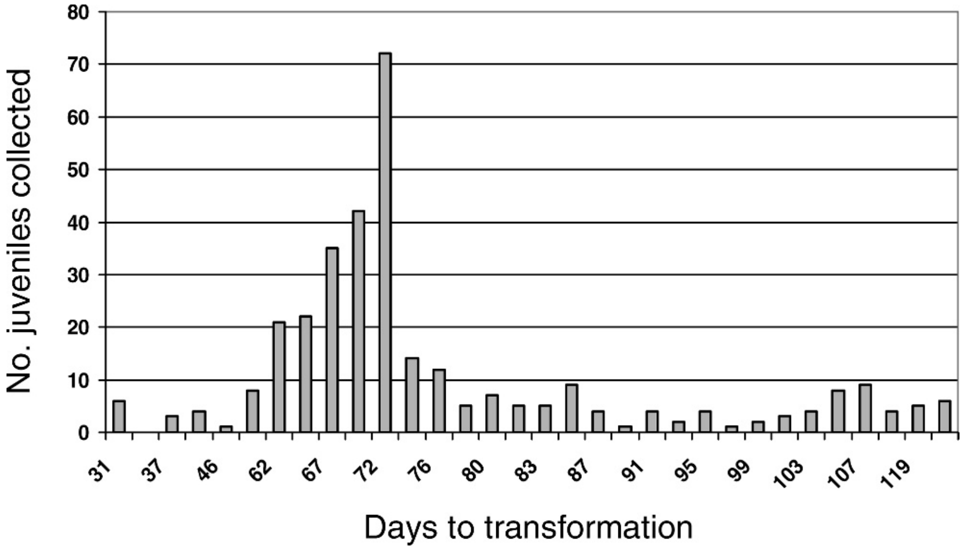

FIG. 3.—Protracted excystment of juveniles of *Lemiox rimosus* from greenside (n = 5) and banded (n = 15) darters. Glochidia were infested on these hosts in the fall of the year (Nov.) (*see* Table 3 for details)

rare in the population (Fig. 5). Older individuals likely exist in the population, but their occurrence is seemingly uncommon and not detected in this limited sample. The predominance of younger individuals indicates that the population has been recruiting in the last 5 y. In the Clinch and Duck rivers respectively, sex ratio was 2:1 and 3:1 in favor of males.

Densities of *Lemiox rimosus* in the Clinch River, TN, were at constant but low levels of $\leq 0.3\ m^{-2}$ from 1979–2004 (Fig. 6). Based on data collected annually by systematic surveys at four sites from 2004–2007, densities were at similar levels, and corresponding population sizes ranged from 210 to 4003 individuals/site (Table 5). By comparison, densities in the Duck River, TN, were at higher levels, ranging from 0.57 to 6.0 m^{-2} from 1979–2004, with a significant ($P = 0.011$) increase observed from 1988 to 2004 (Fig. 6). However, based on data collected by systematic surveys at three sites from 2004–2006, to include Lillard Mill, reported densities were lower and ranged from 0.6 to 1.0 m^{-2}; corresponding population sizes were from 2925 to 29,400 individuals/site (Table 5).

DISCUSSION

Mussel-host fish interactions and life history.—Previous host tests conducted by Hill (1986) and Watson (1999) found that several darter species served as suitable hosts for the glochidia of *L. rimosus* and that other families, including minnows (cyprinids), suckers (catostomids), and catfishes (ictalurids), were unsuitable hosts. Based on juvenile transformation success of previous studies and ours, the primary natural fish hosts are likely *Etheostoma blennioides*, *E. simoterum* and *E. zonale*. These darters are morphologically similar and phylogenetically related [all in the subgenus *Ulocentra*, Porter *et al.* (2002)], with the former two species known to feed on snails (Jenkins and Burkhead, 1994). However, a weakness of this study is that fish host tests were conducted using fish species from only the upper Tennessee River drainage. Thus, additional trials using fish from the Duck River and other streams could reveal additional suitable hosts.

The thick cartilaginous lips and jaw structure of *Etheostoma blennioides* may be adapted to feeding on snails (Jenkins and Burkhead, 1994). During fish host trials, fish were fed adult-sized snail species in the genera *Leptoxis* and *Elimia*, and their feeding behavior directly observed. A darter would quickly take a snail in its mouth, turn it to hold the operculum end, and then suck the soft-body of the snail out of the shell, all in a matter of seconds. In addition, by supplementing its diet with snails while in captivity, its condition and survival improved, suggesting a preference and specialization for feeding on snails. Thus, host-usage by *Lemiox rimosus* seems to be relatively specific, as transformation success on other darter species *i.e.*, *E. rufilineatum* and *E. camurum* which belong to the subgenus *Nothonotus*, generally was poor (Table 3). To our knowledge, *L. rimosus* is the only unionid that has a mantle-lure display that mimics a freshwater snail.

Since females of *Lemiox rimosus* were observed displaying in the fall, it is likely that some glochidia are released and attach to host fishes during this season. Our fish host results showed that juvenile excystment was protracted for trials conducted in the fall. This delayed excystment possibly indicates that glochidia were not completely mature. For example, immature glochidia have been observed in the fall in several other lampsiline mussel species, including *Cyprogenia stegaria*, *Dromus dromas* and *Epioblasma capsaeformis* (Jones and Neves, 2002; Jones *et al.*, 2004, 2005). Why would a female display and release glochidia in the fall that are not completely mature? Do the glochidia continue to mature while they are encysted and over-winter on their host? Over-wintering of glochidia on host fishes already has been documented in *Lampsilis cardium* and other species (*see* Watters and O'Dee, 1999 and references therein), and presents an intriguing possibility for *L. rimosus.* Watters and O'Dee (1999) have shown that prolonged, cold water temperature (*e.g.*, <10 C) was likely the controlling mechanism allowing for delayed excystment and over-wintering on host fish. We suggest that larval maturity may play a role as well, allowing glochidia to delay metamorphosis, then excyst and settle during better growing conditions in the spring to maximize 1st year growth.

Age and growth.—Although maximum age recorded for *Lemiox rimosus* was 15 y, it is possible that older animals may occur in both populations. However, locating older individuals in mussel populations is difficult due to their rarity. The predicted growth increments and *k*-values in the Duck River population were higher than those in the Clinch River population. Biologists have long recognized the greater shell growth and productivity of mussels in the Duck River compared to other rivers in the Tennessee River system (Ortmann, 1924). The headwaters originate in the Highland Rim of the Cumberland Plateau and flow through various sedimentary layers of nutrient-rich siliceous limestone (Ortmann, 1924). Greater mussel growth and productivity likely are due to the more eutrophic conditions generated by these rich sedimentary beds and the natural phosphates they contain. Other factors such as differences in seasonal water temperatures between rivers and population genetics also could play a role. However, the maximum observed lengths and ages converge for both populations at nearly identical values, perhaps indicating that genetically-based physiological differences are not the major factor controlling observed growth differences between populations.

Aging live mussels by using the length-at-age growth curve method should be conducted with caution. Predicted ages of larger and older individuals are less accurate as the slope of the curve decreases at its asymptote. As mussels reach older ages, annual growth increments can be miniscule (<1 mm), and shell growth becomes more variable, making predicted ages

TABLE 4.—Observed and predicted shell lengths at internal annuli of *Lemiox rimosus* from the Clinch and Duck rivers. Number of individuals in parentheses is the sample size of back-calculated lengths-at-ages

Internal annulus (age)	River	Sex	No. of individuals	Observed length (mm)		Predicted length (mm)	Growth increment (mm)
				Mean	Range		
0	Clinch	Male	5 (5)	9.4	7.3–11.8	11.8	11.8
		Female	5 (5)	8.3	5.4–10.7	9.5	9.5
	Duck	Male	5 (5)	8.2	6.0–10.4	8.8	8.8
		Female	5 (5)	7.7	6.5–10.1	8.2	8.2
1	Clinch	Male	5 (5)	15.4	13.0–19.0	16.4	4.6
		Female	5 (5)	17.0	14.6–18.5	16.0	6.5
	Duck	Male	5 (5)	18.3	15.7–20.1	19.1	10.3
		Female	5 (5)	18.2	14.0–23.1	18.1	9.9
2	Clinch	Male	5 (5)	22.4	20.2–25.1	20.6	4.2
		Female	5 (5)	22.2	19.7–24.1	20.9	4.9
	Duck	Male	5 (3)	29.2	23.5–36.3	27.1	8.0
		Female	6 (5)	25.9	21.7–28.7	24.7	6.6
3	Clinch	Male	5 (5)	27.2	23.3–29.4	24.6	4.0
		Female	5 (4)	25.2	23.1–27.0	24.5	3.6
	Duck	Male	5 (5)	33.7	30.2–35.8	33.5	6.4
		Female	6 (5)	30.3	27.2–32.5	29.2	4.5
4	Clinch	Male	5 (2)	31.0	28.5–33.0	28.3	3.7
		Female	5 (4)	27.5	26.0–30.4	27.2	2.7
	Duck	Male	5 (4)	39.9	36.0–43.9	38.4	4.9
		Female	6 (5)	31.7	29.8–34.4	32.2	3.0
5	Clinch	Male	5 (2)	32.1	30.0–35.4	31.8	3.5
		Female	5 (3)	27.5	26.6–28.2	29.2	2.0
	Duck	Male	5 (4)	41.9	38.2–45.2	42.3	3.9
		Female	5 (5)	32.8	31.0–35.4	34.1	1.9
6	Clinch	Male	5 (5)	37.2	35.5–39.0	35.0	3.2
		Female	3 (2)	29.1	28.1–29.7	30.6	1.4
	Duck	Male	5 (4)	43.7	38.4–47.6	45.3	3.0
		Female	5 (4)	34.1	31.6–36.9	35.5	1.4
7	Clinch	Male	5 (1)	36.0	35.0–37.0	38.0	3.0
		Female	3 (2)	30.3	29.5–30.8	31.7	1.1
	Duck	Male	7 (0)	45.6	43.5–48.6	47.7	2.4
		Female	5 (4)	35.5	34.3–37.1	36.4	0.9
8	Clinch	Male	5 (0)	37.5	32.9–40.0	40.7	2.7
		Female	4 (2)	33.1	30.8–38	32.5	0.8
	Duck	Male	6 (0)	49.6	44.9–53.8	49.5	1.8
		Female	6 (3)	36.5	35.3–38.4	37.0	0.6
9	Clinch	Male	7 (0)	40.0	33–44	43.3	2.6
		Female	2 (1)	30.6	30.5–30.8	33.2	0.7
	Duck	Male	8 (8)	52.8	45.6–59.4	51.0	1.5
		Female	4 (3)	37.3	36.2–39.1	37.4	0.4
10	Clinch	Male	4 (0)	42.5	40.0–47.0	45.7	2.4
		Female	1 (1)	34.5	34.5	33.6	0.4
	Duck	Male	7 (0)	50.7	46.9–55.3	52.1	1.1
		Female	3 (2)	39.4	36.5–43.8	37.6	0.2
11	Clinch	Male	4 (2)	49.2	46.0–53.0	47.9	2.2
		Female	1 (0)	35.2	35.2	33.9	0.3

TABLE 4.—Continued

Internal annulus (age)	River	Sex	No. of individuals	Observed length (mm)		Predicted length (mm)	Growth increment (mm)
				Mean	Range		
	Duck	Male	7 (0)	50.9	42.5–59.3	53.0	0.9
		Female	1 (0)	38.7	38.7	37.8	0.2
12	Clinch	Male	2 (2)	52.6	51.3–53.9	50.0	2.1
	Duck	Male	5 (0)	57.3	53.2–58.7	53.7	0.7
13	Clinch	Male	2 (1)	53.1	52.0–54.2	52.0	2.0
	Duck	Male	4 (3)	52.6	48.1–57.2	54.3	0.6
14	Clinch	Male	1 (1)	54.7	54.7	53.7	1.7
	Duck	Male	5 (2)	53.8	48.7–57.2	54.7	0.4
15	Clinch	Male	1 (0)	55.0	55.0	55.4	1.7
	Duck	Male	2 (0)	57.4	57.2–57.5	55.1	0.4

of older individuals less certain. Predicted ages of live mussels can be checked by counting external growth-rings to see whether the two methods are in agreement. External counts typically underestimate ages of older individuals and can be inaccurate if false annuli are counted (Jones and Neves, 2002). Aging mussels by external growth-rings also should be conducted carefully and be corroborated by length-at-age measurements obtained from internal annuli to understand population-specific growth patterns. In most studies, sacrifice of live mussels to estimate population age-class structure is unnecessary and would not be permitted for an endangered species. Hence, both methods can be used together to provide reasonably accurate age estimates of live individuals, especially for younger individuals (<5 y), and document important demographic processes and characteristics, such as recruitment, maximum size and maximum age.

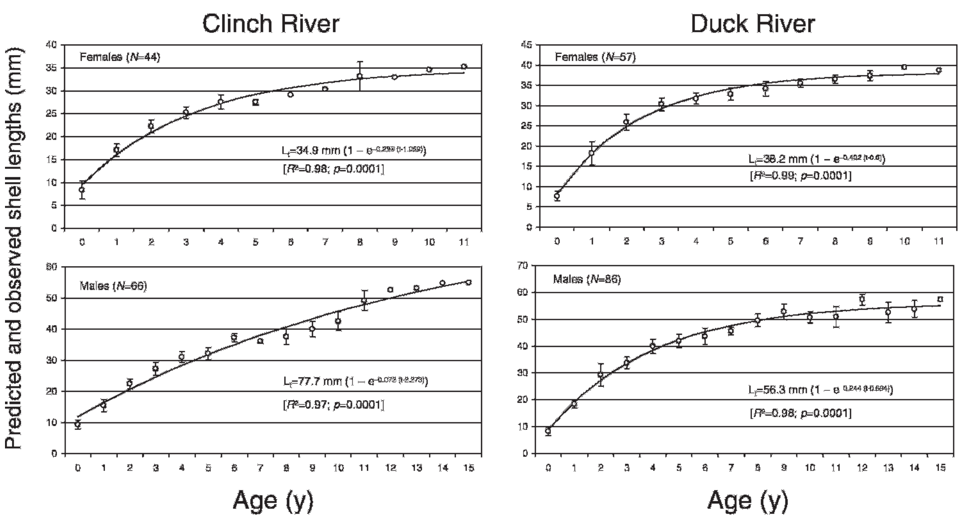

FIG. 4.—Estimated von Bertalanffy growth curves for *Lemiox rimosus* populations showing predicted shell length-at-age. Observed mean length-at-age data are displayed as open circles, along with 95% confidence intervals (CI). Mean values without CI indicate samples sizes of ≤ 3. Total sample sizes (N) are given, which include back-calculated length-at-age data (*see* Results)

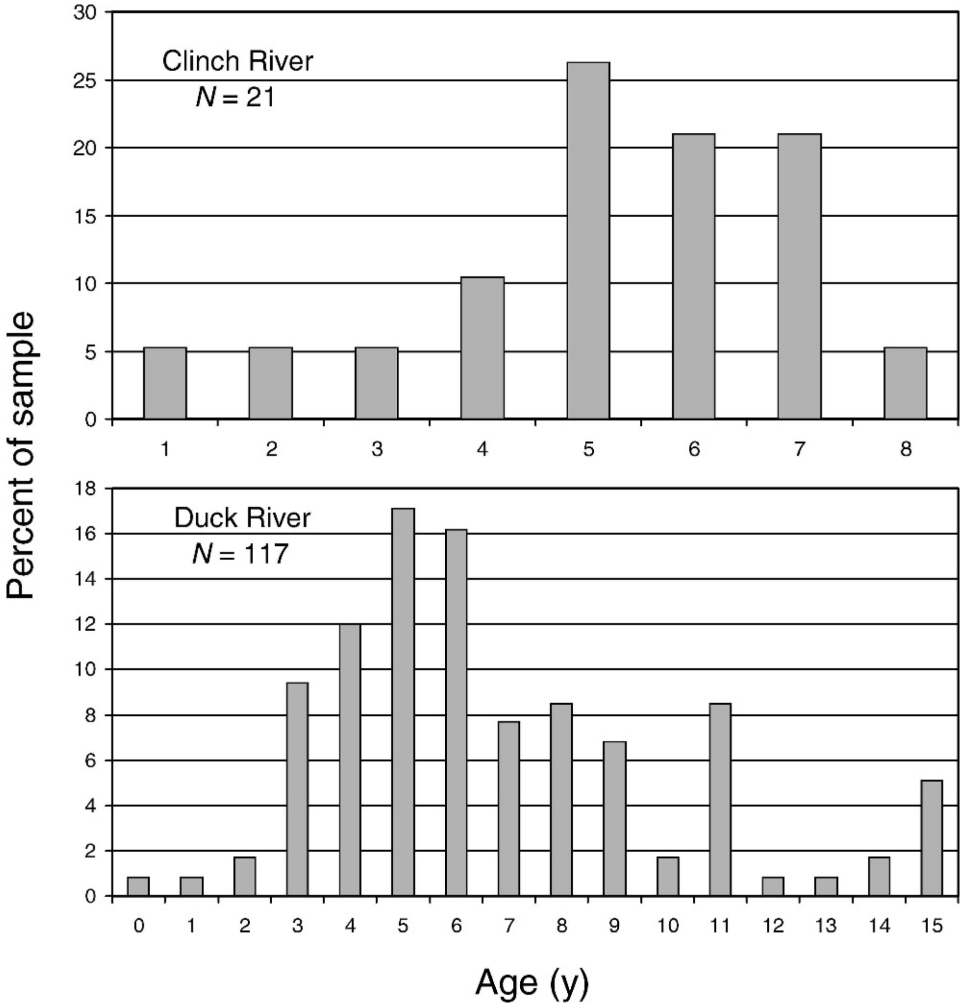

FIG. 5.—Age-frequency histograms of *Lemiox rimosus* populations in the Clinch and Duck rivers; sex ratio was 2:1 and 3:1 in favor of males, respectively

Population trends and juvenile recruitment.—Most of the live specimens found in both rivers between 2004 and 2007 were of small and medium sizes, indicating that these populations are recruiting. Age histograms showed multiple age classes of young mussels (1–3 y), collectively comprising about 16% of sampled individuals in the Clinch River, and about 12% in the Duck River (Fig. 4). Furthermore, the time-series of historical densities of *Lemiox rimosus* from 1979–2004 reported by Ahlstedt *et al.* (2004, 2005) indicated stable or increasing population trends in each river, respectively (Fig. 6). Although these data were collected using a different sampling design, the protocol was implemented consistently at each time interval, thus providing additional insights into density trends over longer time periods. However, because the protocol sampled areas of best available habitat, density may have been over-estimated relative to total available habitat. Increasing abundance of *L.*

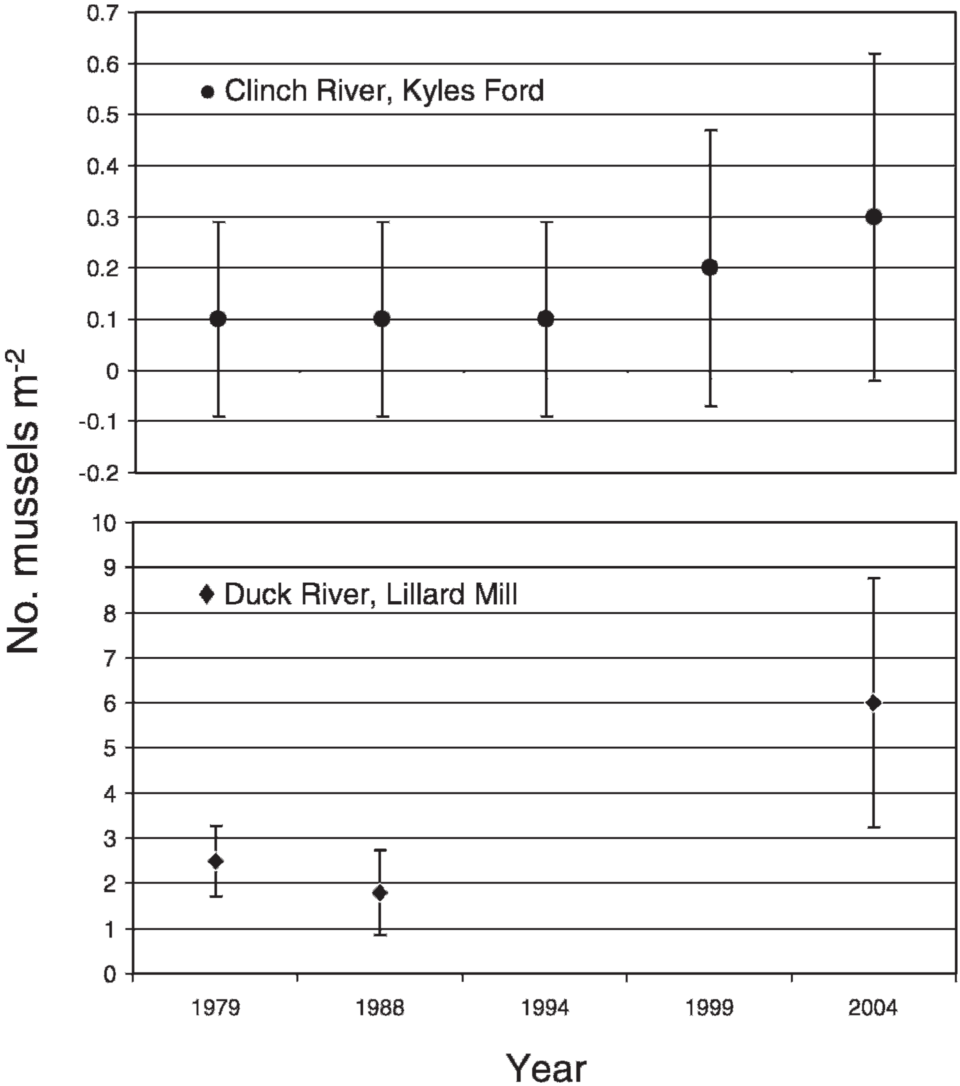

FIG. 6.—Historical densities of *Lemiox rimosus* from 1979–2004 in the Clinch River at Kyles Ford, TN and Duck River at Lillard Mill, TN; these are sites where the highest abundance and density of the species typically occurs in each river. Data are from Ahlstedt *et al.* (2004, 2005)

rimosus and other mussel species in the Duck River during the past 15–20 y is attributed primarily to reservoir release improvements (RRI) at the TVA's Normandy Dam (River Kilometer 402) near Normandy, TN (Ahlstedt *et al.*, 2004). The RRI was initiated in 1991 to improve minimum flows and dissolved oxygen levels in the river.

Mortality is a dynamic process and can be difficult to assess. The unequal sex ratios and shorter longevity of females observed in this study suggest that female mortality is higher, perhaps due to reproductive stress and increased predation during mantle-lure display and the release of glochidia.

TABLE 5.—Locality and population density data of *Lemiox rimosus* at selected sites in the Clinch and Duck rivers, TN. ND = individuals not detected in quadrat samples and NC = not calculated

Site locations	River kilometer	Year (s) sampled	Quadrats sampled y^{-1} (n)	Number collected	Density m^{-2} (SD)	Site area (m^{-2})	Population size (95% CI)
Clinch River:							
Wallen Bend (upper)	309.6	2004[a]	60	1	0.066 (0.516)	3183	210 (±415)
		2005[a]	60	0	ND		NC
		2006[a]	60	1	0.066 (0.516)		210 (±415)
		2007[a]	60	1	0.066 (0.516)		210 (±415)
Kyles Ford	305.2	2004[b]	146	7	0.190 (0.976)	15,000	2850 (±2443)
Frost Ford	291.7	2004[a]	60	2	0.133 (0.724)	15,050	2002 (±2756)
		2005[a]	60	1	0.066 (0.516)		993 (±1964)
		2006[a]	60	4	0.266 (1.004)		4003 (±3821)
		2007[a]	60	0	ND		NC
Swan Island	277.2	2004[a]	60	0	ND	5746	NC
		2005[a]	60	0	ND		NC
		2006[a]	60	1	0.066 (0.516)		379 (±750)
		2007[a]	60	0	ND		NC
Duck River:							
Lillard Mill	288.0	2006[c]	254	90	1.42 (4.485)	22,500	22,500 (±3931)
Venable Spring	285.3	2004[d]	285	46	0.650*	4500	2925
Hooper Island	262.3	2006[c]	169	27	0.639 (1.594)	49,000	29,400 (±11,776)

[a] Jones, J.W. 2004–2007. U.S. Fish and Wildlife Service, unpublished data
[b] Ostby, B.J.K. 2005
[c] Ostby, B.J.K., and R.J. Neves. 2007
[d] Adair, B.D. 2005
* Standard deviation was not available, but likely similar to samples collected at Hooper Island

Based on current population structure and trends, we believe that both the Clinch and Duck river populations of *Lemiox rimosus* are experiencing recruitment and are currently stable. These populations should remain viable as long as habitat, water quality and ecological conditions are maintained in these rivers. The Clinch River population has been at low densities ($<0.5\ m^{-2}$) for several decades, a trend that is likely to continue. Interestingly, Ortmann (1918) considered the species rare in the river in the early 1900s. Hence, the rarity of the species is seemingly natural, making monitoring a challenge. Finally, a remnant population of *L. rimosus* still resides in the Powell River in Tennessee and Virginia. Individuals occur at very low densities ($<0.01\ m^{-2}$) at sites of occurrence, but gravid females and young adults (≤ 4 y) recently (2004–2007) have been observed in the river. The viability of this population is unknown, but evidence of gravidity and recruitment is encouraging.

Conservation recommendations.—Recovery of *Lemiox rimosus* will require protection and expansion of existing populations, and establishment of additional populations into historically occupied habitat. A genetic analysis is needed to determine whether levels of divergence between the Clinch and Duck river populations warrant separate management units. However, utilizing the high abundance in the latter population as broodstock represents the best opportunity to recover the species throughout the Tennessee River basin. Therefore, it is critical that water releases from Normandy Dam be maintained at flow and temperature levels that will continue to produce sustainable population recruitment of the species in the river.

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