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REGULAR ARTICLE

QUANTITATIVE MONITORING OF FRESHWATER MUSSEL POPULATIONS FROM 1979–2004 IN THE CLINCH AND POWELL RIVERS OF TENNESSEE AND VIRGINIA, WITH MISCELLANEOUS NOTES ON THE FAUNA

Steven A. Ahlstedt¹, Mark T. Fagg², Robert S. Butler³, Joseph F. Connell⁴, and Jess W. Jones^{5*}

ABSTRACT

The Clinch and Powell rivers, Tennessee (TN) and Virginia (VA), upstream of Norris Reservoir, TN, are known for high freshwater mussel species diversity and endemism. Collectively, these rivers harbored at least 56 species historically and 49 are extant, many of which now survive only in the Clinch or Powell rivers or a few other streams. Among an unparalleled 24 federally endangered mussel species known from these rivers, 20 species are considered extant. We sampled 0.25 m⁻² quadrats at six Clinch River sites and four Powell River sites for a total of 4–6 sample years at each site. Overall trends were highly significant in the Clinch River, with mean mussel density at combined sites in each state increasing from 16.5 m⁻² to 41.7 m⁻² (p < 0.0001) at sites in TN but declining from 12.0 m⁻² to 3.3 m⁻² (p < 0.001) at sites in VA. Cumulative species richness was 39, ranging from 36 in TN to 27 in VA. Greater density in the Clinch River, TN, was due primarily to increases in *Epioblasma capsaeformis*, *Medionidus conradicus*, and *Ptychobranchus subtentus*, which were rare or undetected at most sites in 1979, but increased five- to ten-fold by 2004. Conversely, at Pendleton Island, VA, which was the best site for mussels in the river circa 1980, the decline in density was highly significant, from 24.6 m⁻² in 1979 to 4.6 m⁻² (p < 0.001) in 2004. In the Powell River, there was also a highly significant decline in mean mussel density at combined sites from 8.7 m⁻² to 3.3 m⁻² (p < 0.001), with a total of 33 species documented. Though species diversity remains relatively high, our results confirm that mussel populations have declined in large reaches of each river over the 25-year study period.

KEY WORDS - Clinch and Powell rivers; biodiversity hotspot; freshwater mussels; endangered species; mussel population declines.

INTRODUCTION

The Clinch River and its largest tributary Powell River are located in northeastern TN and southwestern VA and are part of the upper Tennessee River drainage (Figure 1). The Tennessee River drainage supports the highest freshwater mussel diversity

of any comparably-sized river system in the world. More than 105 species are known from this drainage, with at least 36 species endemic to it or shared only with the Cumberland River drainage (Parmalee and Bogan 1998). Collectively, upland portions of these two drainages are known as the Tennessee-Cumberland Province (Haag 2010). Mussel diversity was highest in the mainstem Tennessee River and its large tributaries, but impoundments created during the 1920s through

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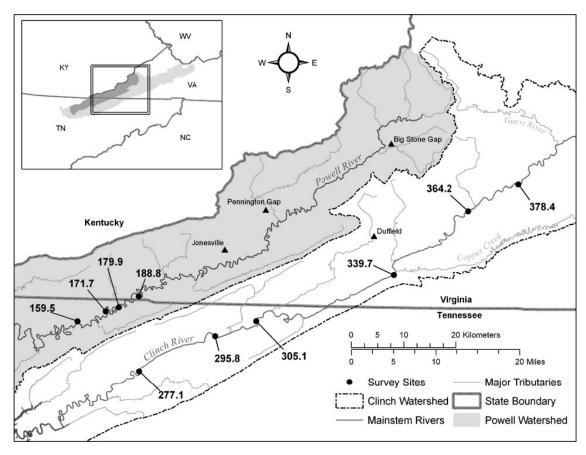


Figure 1. The Clinch and Powell river watersheds showing locations of sites (in RKM) sampled from 1979-2004.

1970s destroyed most large-river habitats (Haag 2009). The lower Clinch River was impounded by Watts Bar Dam on the Tennessee River, and Melton Hill and Norris dams on the Clinch River (river km [RKM] 37.0 and 128.5, respectively). Norris Dam impounds the river to about river km 249 as well as the lower 90 km of the Powell River, and the dam effectively isolated these two rivers and eradicated at least 10 additional species from the drainage (Ortmann 1918; Ahlstedt 1991a). Nevertheless, the free-flowing upper reaches of the Clinch and Powell rivers are among the most important remaining riverine habitats in the Tennessee River drainage, and they support a large percentage of the surviving mussel fauna of the region (Johnson et al. 2012; Jones et al. 2014).

Among the 56 species known historically from the Clinch and Powell river mainstems upstream of Norris Reservoir, 24 are now federally endangered under the Endangered Species Act (ESA), though 4 of these listed species are considered extinct or extirpated from these rivers (Table 1). Further, an additional seven of the extant species are included in a petition for possible federal listing. The Clinch River harbors the largest remaining population (namely, *Dromus dromas*, *Epioblasma brevidens*, *E. capsaeformis*, *Fusconaia cor*, *F. cuneolus*, *Hemistena lata*, *Ptychobranchus subtentus*, *Quadrula cylindrica strigillata*), or one of the few existing populations (e.g., *Cyprogenia*)

stegaria, E. florentina aureola, Lemiox rimosus, Pegias fabula, Pleurobema plenum, Q. sparsa, Venustaconcha trabalis [studies by Kuehnl (2009) and Lane et al. (2016) have shown that Villosa trabalis belongs in the genus Venustaconcha, and that Villosa perpurpurea is a synonym; see Discussion]), of 15 endangered mussels, in addition to large populations of several other imperiled species (Jones et al. 2014; Table 1). Fifteen of 19 endangered species are considered extant in the Powell River, which itself harbors 1 of only 2 extant populations of D. dromas, Q. cylindrica strigillata, Q. intermedia, and Q. sparsa (Johnson et al. 2012).

Various malacologists have reported on the mussels in the Clinch and Powell rivers over the last century. Arnold E. Ortmann (1918), Carnegie Museum, Pittsburgh, Pennsylvania, reported the only systematic pre-impoundment collection records in the study area, including several records from Adams (1915). In the 1960s and 1970s, David H. Stansbery, Ohio State University Museum of Biological Diversity, Columbus, Ohio, and his students made scores of collections in the study area, documenting declines in species richness since Ortmann's (1918) collections, many from areas now inundated by Norris Reservoir (Stansbery 1973). Greater survey effort and interest in conserving the mussel fauna accelerated in the mid-1970s following passage of the ESA in

Table 1. Scientific names, and federal and Freshwater Mollusk Conservation Society (FMCS; J.D. Williams, Florida Museum of Natural History, unpub. data) status of mussel species known from the Clinch and Powell river mainstems upstream of Norris Reservoir in TN and VA. $\sqrt{\ }$ extant and sampled during our study, $\sqrt{\ }$ extant but not sampled or recognized during our study, * every rare, - eno federal status, CS = currently stable, E = endangered, EX = extirpated, FE = federally endangered, NR = not reported, P = petitioned for federal listing, RI = sampled during our study and subsequently considered extirpated but now extant from reintroduction, T = threatened, V = vulnerable, and X = extinct. Species list and study area status updated from Johnson et al. (2012) and Jones et al. (2014).

Scientific Name	Clinch	Powell	Federal	FMCS
(1) Actinonaias ligamentina	\checkmark	\checkmark	-	CS
(2) Actinonaias pectorosa	$\sqrt{}$	$\sqrt{}$	-	T
(3) Alasmidonta marginata	$\sqrt{*}$	$\sqrt{*}$	-	V
(4) Alasmidonta viridis	$\sqrt{x^*}$	NR	-	V
(5) Amblema plicata	$\sqrt{}$	$\sqrt{}$	-	CS
(6) Anodontoides ferrusacianus	NR	EX	-	CS
(7) Cumberlandia monodonta	$\sqrt{}$	$\sqrt{x^*}$	FE	E
(8) Cyclonaias tuberculata	$\sqrt{}$	\checkmark	-	V
(9) Cyprogenia stegaria	$\sqrt{}$	EX	FE	E
(10) Dromus dromas	$\sqrt{}$	$\sqrt{}$	FE	E
(11) Elliptio crassidens	$\sqrt{*}$	$\sqrt{*}$	-	V
(12) Elliptio dilatata	$\sqrt{}$	$\sqrt{}$	-	V
(13) Epioblasma brevidens	$\sqrt{}$	$\sqrt{}$	FE	E
(14) Epioblasma capsaeformis		\sqrt{RI}	FE	E
(15) Epioblasma florentina aureola	\sqrt{x}	NR	FE	E
(16) Epioblasma haysiana	X	X	-	X
(17) Epioblasma lenior	X	X	-	X
(18) Epioblasma torulosa gubernaculum	X	X	FE	X
(19) Epioblasma triquetra	$\sqrt{}$	$\sqrt{*}$	FE	T
(20) Fusconaia cor	V	· *	FE	Е
(21) Fusconaia cuneolus	V	· *	FE	Е
(22) Fusconaia subrotunda	V	· 	P	Е
(23) Hemistena lata	V	\sqrt{x}	FE	Е
(24) Lampsilis abrupta	\sqrt{x}	NR	FE	T
(25) Lampsilis fasciola	· V	$\sqrt{}$	-	CS
(26) Lampsilis ovata	V	V	-	V
(27) Lasmigona costata	V	V	-	CS
(28) Lasmigona holstonia	$\sqrt{x^*}$	EX	P	V
(29) Lemiox rimosus		$\sqrt{*}$	FE	Е
(30) Leptodea fragilis	EX	EX	-	CS
(31) Leptodea leptodon	EX	NR	FE	Е
(32) Ligumia recta	$\sqrt{*}$	$\sqrt{*}$	-	V
(33) Medionidus conradicus	V		P	T
(34) Pegias fabula	√x*	EX	FE	Е
(35) Plethobasus cyphyus	· 	$\sqrt{}$	FE	Е
(36) Pleurobema cordatum		NR	-	V
(37) Pleurobema oviforme	V	$\sqrt{*}$	P	T
(38) Pleurobema plenum	V	NR	FE	Е
(39) Pleurobema rubrum	V	NR	P	Е
(40) Pleurobema sintoxia	√x*	NR	-	V
(41) Pleuronaia barnesiana	V	*	P	V
(42) Pleuronaia dolabelloides	v	v √*	FE	E
(43) Potamilus alatus	v	v *	-	CS
(44) Ptychobranchus fasciolaris	v V	v √	-	V
(45) Ptychobranchus subtentus	V	v V	FE	Ē
(46) Quadrula cylindrica strigillata	V	v √	FE	E
(47) Quadrula intermedia	EX	v V	FE	E
(48) Quadrula pustulosa	V	V	-	CS

Table 1, continued.

Scientific Name	Clinch	Powell	Federal	FMCS
(49) Quadrula sparsa	$\sqrt{_{ m X}}^*$	\checkmark	FE	Е
(50) Strophitus undulatus	\sqrt{x}	$\sqrt{x^*}$	-	CS
(51) Toxolasma lividum	$\sqrt{x^*}$	EX	P	V
(52) Truncilla truncata	$\sqrt{*}$	$\sqrt{x^*}$	-	CS
(53) Venustaconcha trabalis	$\sqrt{*}$	EX	FE	E
(54) Villosa fabalis	EX	NR	FE	E
(55) Villosa iris	$\sqrt{}$	$\sqrt{}$	-	CS
(56) Villosa vanuxemensis	$\sqrt{}$	$\sqrt{}$	-	V
Total Species Known	55	47		
Total Species Extant	48	37		
Total Species Extant Sampled 1979–2004	39	33		
Total Listed Species Known	24	19		
Total Listed Species Extant	20	15		
Total FMCS Imperiled Species Extant	39	28		

1973. These surveys include the Clinch River (Stansbery 1973; Bates and Dennis 1978; Stansbery et al. 1986; Dennis 1989; Ahlstedt 1991a; Church 1991; Jones et al. 2014), the Powell River (Ahlstedt and Brown 1979; Dennis 1981; Ahlstedt 1991b; Wolcott and Neves 1994; Johnson et al. 2012), or both rivers (Neves et al. 1980; Dennis 1985; Ahlstedt and Tuberville 1997).

The goal of our study was to quantify changes in the mussel fauna of the upper Clinch and Powell rivers over a 25-y period (1979–2004). Our primary objective was to quantitatively sample multiple fixed sites in both rivers and evaluate species richness, density and population trends during this period. Secondary objectives were to: 1) compare our results with previous and more recent collection data, 2) compile a comprehensive list of mussels known from the study area and their conservation status, and 3) generate a timeline of anthropogenic impacts that have potentially affected the status of the fauna during the past and into the future.

METHODS

Study Area

The watersheds of the Clinch River and its tributary Powell River form a large portion of the headwaters of the upper Tennessee River drainage in northeastern TN and southwestern VA (Figure 1). These drainages occur primarily in the Ridge and Valley Physiographic Province, with a small portion in the Appalachian Plateaus Physiographic Province in VA. The study area incorporates the free-flowing mainstems of these rivers upstream of Norris Reservoir, TN. The upper Clinch River watershed contains an area of 3,721 km², while the upper Powell River watershed contains 2,471 km². Land cover is primarily agriculture and mixed forest, with small towns scattered in the drainages and fossil fuel extraction in the Appalachian Plateaus headwaters. Industry is limited, but

two coal-fired power plants are located on the upper Clinch River.

Site Selection and Sampling Methodology

We selected sampling sites during float surveys via canoe and small watercraft in 1979 (Ahlstedt 1991a, b; Table 2; Figure 1). Selected sites had aggregations of mussels in shoals—habitat patches having shallow water and swift flows over primarily gravel and cobble substrates—that also offered easy access. We identified sampling sites by RKM and landmarks on 7.5-minute topographic maps. We initially selected 11 sites on the Clinch River and 15 sites on the Powell River (Ahlstedt and Tuberville 1997). However, due to severe mussel declines at some sites, as well as time and funding constraints, sampling sites were reduced to six in the Clinch River (three each in TN and VA) and four in the Powell River (three in TN and one in VA) for data analyses.

Quantitative mussel sampling was conducted by randomly placing 0.25 m^2 quadrats on substrate in the shoal habitat of each site. Using mask and snorkel, surveyors searched for mussels by excavating substrate from quadrats to a depth of ~ 15 cm or until hardpan or bedrock was reached. Once live mussels were identified and recorded, we returned them to the substrate. Over the 25-y period, we conducted four (at Pendleton Island, VA) or five (at all other sites) sampling events at each Clinch River site, and six sampling events at each Powell River site (Table 3; Appendices I and II).

Data Analysis

We calculated mean density for each species and the assemblage at each site and year of sampling (Table 3; Appendices I and II). The 1979 quadrat data from all sites in the Clinch and Powell rivers were not available for analysis, only the mean values per site were available for that year,

Table 2. Location and quadrat sample sizes of the ten long-term fixed-station monitoring sites for mussels in the Clinch and Powell rivers, TN and VA, sampled from 1979–2004.

River/RKM	Site	Lat./Long.	No. Quadrats
Clinch River			
CRKM 277.1	Swan Island, Hancock Co., TN	36.2834N 83.1726W	40
CRKM 295.8	Brooks Island, Hancock Co., TN	36.3216N 83.0739W	26
CRKM 305.1	Kyles Ford, Hancock Co., TN	36.3403N 83.0233W	41
CRKM 339.7	Speers Ferry, Scott Co., VA	36.3858N 82.4455W	40
CRKM 364.2	Pendleton Island, Scott Co., VA	36.4542N 83.3526W	40
CRKM 378.4	Semones Island, Scott Co., VA	36.4833N 82.2905W	40
Powell River			
PRKM 159.5	Buchanan Ford, Claiborne Co., TN	36.3329N 83.2525W	40
PRKM 171.7	McDowell Shoal, Hancock Co., TN	36.3442N 83.2200W	40
PRKM 179.9	Bales Ford, Hancock Co., TN	36.3503N 83.2011W	20
PRKM 188.8	Fletcher Ford, Lee Co., VA	36.3614N 83.1741W	42

which were previously recorded by Ahlstedt and Tuberville (1997). Hence, all analyses were restricted to mean density values per site and year. We used a generalized linear model (GLM) to test for significance of trends in mean density of the mussel assemblage over time to make four comparisons: 1) sites in the Clinch River, VA; 2) sites in the Clinch River, TN; 3) Pendleton Island, VA; and 4) sites in the Powell River, TN and VA (Figure 2). We implemented the GLM

using a Poisson distribution and log link function in the program R (R Development Core Team 2006) and test results were considered significant at α =0.05. Mean density values of the portion of our study from 1979–1994 were reported by Ahlstedt and Tuberville (1997). Mean mussel density at Pendleton Island in 1987 was obtained from Dennis (1989), who used similar sampling methods as our study.

Table 3. Mussels per meter squared, number of species, number of endangered species, mean values and associated 95% confidence intervals (CI) for sampling sites in the Clinch and Powell rivers, TN and VA, sampled from 1979–2004. Non-overlapping CI's among sites in each respective river are significantly different at the 0.05 alpha level. Numbers in parentheses under each site location are the total number of species collected at the site over the study.

				San	nple Year			
	1979	1983	1988	1994	1999	2004	Mean	±95% CI
Clinch River Site (CRKM)								
Swan Island, TN (CRKM 277.	1)							
Per meter squared	7.0	-	1.6	10.6	11.4	29.4	12.0	9.2
Species (23)	11	-	9	17	16	17	14.0	3.3
Endangered Species (8)	4	-	3	6	7	6	5.2	1.4
Brooks Island, TN (CRKM 29:	5.8)							
Per meter squared	11.4	-	9.7	13.7	40.8	21.3	19.4	11.2
Species (29)	15	-	10	15	16	20	15.2	3.1
Endangered Species (10)	4	-	3	6	5	7	5.0	1.4
Kyles Ford, TN (CRKM 305.1)							
Per meter squared	31.0	-	14.1	37.6	95.9	74.3	50.6	29.3
Species (31)	27	-	19	20	23	23	22.4	2.7
Endangered Species (12)	11	-	7	8	10	11	9.4	1.6
Speers Ferry, VA (CRKM 339	.7)							
Per meter squared	3.7	-	2.7	2.9	4.8	3.7	3.6	0.7
Species (22)	11	-	13	10	9	10	10.6	1.3
Endangered Species (8)	3	-	4	2	2	4	3.0	0.9
Pendleton Island, VA (CRKM	364.2)							
Per meter squared	24.6	-	-	11.2	12.4	4.6	13.2	7.3
Species (23)	21	-	-	13	13	10	14.3	4.1
Endangered Species (6)	6			3	2	1	3.0	1.9

Table 3, continued.

				San	nple Year			
	1979	1983	1988	1994	1999	2004	Mean	±95% CI
Semones Island, VA (CRKM	378.4)							
Per meter squared	_	7.7	4.6	6.5	4.2	1.7	4.9	2.0
Species (17)	-	14	11	10	9	6	10.0	2.6
Endangered Species (5)	-	2	3	2	1	1	1.8	0.7
Powell River Site (PRKM)								
Buchanan Ford, TN (PRKM 1	159.5)							
Per meter squared	10.9	21.8	3.5	5.5	5.1	8.0	9.1	5.4
Species (24)	14	15	7	9	7	11	10.5	2.8
Endangered Species (8)	2	5	-	2	2	1	2.4	1.2
McDowell Shoal, TN (PRKM	171.7)							
Per meter squared	5.5	2.3	3.3	1.8	2.8	1.4	2.9	1.2
Species (22)	16	10	13	8	10	7	10.7	2.7
Endangered Species (8)	6	2	3	1	1	1	2.3	1.6
Bales Ford, TN (PRKM 179.9	9)							
Per meter squared	7.2	4.8	2.6	4.4	4.2	2.2	4.2	1.4
Species (19)	12	8	8	10	9	6	8.8	1.6
Endangered Species (7)	4	2	2	4	2	1	2.5	1.0
Fletcher Ford, VA (PRKM 18	(8.8)							
Per meter squared	11.2	10.3	5.6	7.0	5.2	1.4	6.8	2.9
Species (23)	16	14	11	10	8	7	11.0	2.8
Endangered Species (8)	4	3	2	2	2	1	2.3	0.8

Conservation Status of the Fauna

We compiled a comprehensive list of mussels known from the upper Clinch and Powell river mainstems based on published literature and other records (Table 1). This list includes the population status of each species in the study area, federal status under the U.S. Fish and Wildlife Service (USFWS), and its global conservation status according to the Freshwater Mollusk Conservation Society (FMCS) (J.D. Williams, Florida Museum of Natural History, unpub, data). Finally, we generated a chronology of anthropogenic impacts from the literature and our personal observations over the last 40 y likely affecting the status of the mussel fauna (Table 4).

RESULTS

Clinch River

At the six study sites, we observed a total of 39 of 55 mussel species (71%) known from the Clinch River mainstem upstream of Norris Reservoir (Table 1; Appendix I). Species richness ranged from 36 in TN to 27 in VA, and among sites from 31 at Kyles Ford, TN, to 17 at Semones Island, VA. Over the sampling period, richness declined from 34 in 1979 to 29 in 2004 (Table 3). No other site yielded as many species during any intervening sampling year as did Kyles Ford,

though richness dropped from 27 in 1979 to 23 species in both 1999 and 2004. Species richness increased from 11 to 17 species at Swan Island, TN, and 15 to 20 species at Brooks Island, TN, from 1979 to 2004. Sites in VA had lower species richness relative to those in TN, with the exception of Pendleton Island, VA, where 21 species were recorded in 1979. However, species richness declined to a low of 10 species at this site in 1999. At Speers Ferry, VA, species richness fluctuated from a high of 13 in 1988 to a low of 9 in 1999, and similarly at Semones Island from a high of 14 in 1988 to a low of 6 in 1999. Mussel diversity in Clinch River included 16 federally endangered species—14 in TN and 8 in VA. Endangered species ranged from 12 (Kyles Ford) to 8 (Swan Island) in TN and 8 (Speers Ferry) to 5 (Semones Island) in VA.

Mean mussel density among all sites combined on the TN side of the Clinch River increased significantly (p < 0.001) from 16.5 m⁻² in 1979 to 41.7 m⁻² in 2004 (Figure 2A). Density at the beginning and end of our study ranged from 7.0 to 29.4 m⁻² at Swan Island, 11.4 to 21.3 m⁻² at Brooks Island, and 31.0 to 74.3 m⁻² at Kyles Ford, respectively, though the increasing trend was not uniform over all sampling periods (Table 3). Conversely, mean mussel density at sites on the VA side decreased significantly (p < 0.001) from 12.0 m⁻² in 1979 to 3.3 m⁻² in 2004 (Figure 2B). Over this period, density essentially remained unchanged at Speers Ferry (3.7 m⁻²) but declined

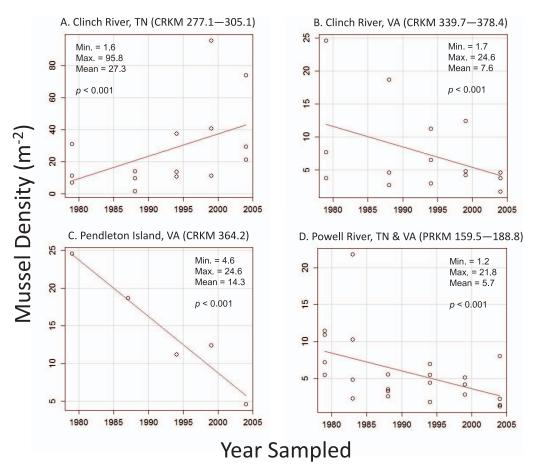


Figure 2. Time series plots and linear regression analyses of mean mussel density from 1979–2004 in reaches and sites in the Clinch and Powell rivers of TN and VA; data were collected using a random survey design. The mean density value of 18.7 mussels m⁻² at Pendleton Island in 1987 was from data collected by Dennis (1989); data shown in panels B and C. Reported *p*-value indicates significance of the mussel density and year sampled trend.

significantly (p < 0.001) at Pendleton Island from 24.6 to 4.6 m⁻² (Figure 2C) and also declined at Semones Island from 7.7 to 1.7 m⁻² (Table 3).

Among species, Actinonaias pectorosa and A. ligamentina dominated overall abundance in the Clinch River at sites in both states (Appendix I). The next three most abundant species in VA were Elliptio dilatata, Fusconaia subrotunda, and Medionidus conradicus, while in TN they were M. conradicus, Ptychobranchus subtentus, and Epioblasma capsaeformis. Ptychobranchus subtentus was by far the most abundant endangered species reported, and was fourth in overall abundance. Peak densities of this species reached 20.3 m⁻² in 1999 and 16.2 m⁻² in 2004 at Kyles Ford. By 2004, the species had become more common at the two other TN sites (>3.0 m⁻² per sample) but remained uncommon at VA sites $(<0.3 \text{ m}^{-2} \text{ per sample})$. Other relatively common listed species ($\sim 1 \text{ m}^{-2}$ per sample) by the end of our study were E. capsaeformis at all three TN sites, Dromus dromas at Swan Island, and *E. triquetra* at Brooks Island.

A total of 55 species are known historically from the Clinch River and we consider 48 species to be extant, including 20 of 24 federally endangered species (Table 1).

Overall, 39 of the extant species in the river are imperiled. The USFWS has been petitioned to list under the ESA seven imperiled species known from and considered extant in the river.

Powell River

At the four sites, we observed a total of 33 of 47 mussel species (70%) known from the mainstem Powell River upstream of Norris Reservoir (Table 1; Appendix II). Species richness was 26 in 1979 but declined to 14 by 2004; among sites, it ranged from 24 at Buchanan Ford, TN, to 19 at Bales Ford, TN (Table 3). Between 1979 and 2004, richness declined from 16 to 7 species at both McDowell Shoal, TN, and Fletcher Ford, VA, and from 12 to 6 species at Bales Ford. At Buchanan Ford the decline was 14 to 11 species. Powell River diversity included 12 endangered species, where each site had eight endangered species except Bales Ford (7 endangered species).

Mean mussel density among all sites combined declined significantly (8.8 to 3.2 m $^{-2}$; p < 0.001) over the study period (Figure 2D) and was most severe at Fletcher Ford (11.2 to 1.4

Table 4. Chronology of some significant perturbations that have occurred in the Clinch and Powell rivers.

Year(s)	Perturbation	Source
1870–1920	The Clinch and Powell river watersheds are initially logged, releasing massive quantities of sediment into the rivers.	Caudill (1963)
Mid to late 1800s	Logs floated downstream in the Clinch and Powell rivers to markets in Knoxville, TN, likely results in shoal habitat disruption and increased sedimentation.	Caudill (1963)
1881	Deep mining for coal begins in southwestern VA.	Hibbard and Clutter (1990)
Late 1800s to early 1900s	Railroads expanded along rivers to haul coal out of southwestern VA.	Eby (1923), Woodward (1936)
1884–1936	Mussels harvested in the Clinch and Powell rivers for natural pearls.	Boëpple and Coker (1912)
1909–1940s	Mussels harvested in the Clinch and Powell rivers for button industry.	Boëpple and Coker (1912)
1913	Discharges of industrial and mine wastes in the upper Clinch and Powell rivers, VA.	Adams (1915), Ortmann (1918)
Beginning in 1900	Extreme soil erosion from row-cropping and other agricultural practices throughout the Clinch and Powell river watersheds.	Caudill (1963), Sagona (1990), Sagona and Carroll (1991), TNC (1992)
1936–1963	Three impoundments (Norris Dam, the lower Clinch River, 1936; Watts Bar Dam, the upper Tennessee River, 1942; Melton Hill Dam, the lower Clinch River, 1963) constructed by Tennessee Valley Authority (TVA) for flood control and electric power production results in major loss or alteration of habitat throughout ~240 kilometers of the lower Clinch River and ~80 kilometers of the lower Powell River, isolating and fragmenting mussel and fish populations, and blocking movements of migratory host fishes.	Cahn (1936), Hickman (1937), Masnik (1974), Ahlstedt and Brown (1979), Ahlstedt (1991a)
1943	Surface mining for coal begins in southwestern VA.	Caudill (1963)
1950s to present	Black-water releases (coal fines) into the Clinch and Powell rivers from preparation plants located in southwestern VA.	Carriker (1981), TN/VA Joint Task Force (1985), TNC (1992)
1960s-1970s	Mussels harvested in the Clinch River for cultured pearl industry.	Tennessee Wildlife Resources Commission Proclamation 80- 14 [1980]
1960s–1970s	Mussels harvested in the Clinch and Powell rivers and sold to biological supply companies for dissection in high school and college biology classes.	Tennessee Wildlife Resources Commission Proclamation 80- 14 [1980]
1967	Massive fly-ash spill from the Clinch River Steam Plant at Carbo, VA, kills thousands of mussels and fishes over ∼120 kilometers of river. Macroinvertebrates largely recover within a few months but mollusks do not.	Cairns et al. (1971), Crossman (1973), Raleigh et al. (1978), Stansbery et al. (1986)
1970s	The Powell River upstream of Pennington Gap, VA, was so adversely affected from coal mining operations that it was dredged to remove contaminants.	EPA (2002)
1970	Sulfuric acid spill from the Clinch River Steam Plant at Carbo, VA, kills thousands of mussels and fishes for ~24 kilometers of river. Fishes and macroinvertebrates largely recover within a few months but mollusks do not.	Cairns et al. (1971), Crossman (1973), Raleigh et al. (1978)
1972	On December 25 th the Powell River was observed black from coal fines.	EPA (2002)
1977	A 100-y flood in the Clinch and Powell rivers strands many mussels along shorelines.	TVA (1978), S.A. Ahlstedt (pers. obs.)

Table 4, continued.

Year(s)	Perturbation	Source
1978	A low-head bridge was constructed after the 100-y flood on McDowell Shoal, the richest mussel shoal habitat in the Powell River, TN. This bridge was washed-out in 1979 and removed from the river, highly destabilizing shoal habitat.	S.A. Ahlstedt (pers. obs.)
1979	Black-water releases were observed draining into the Clinch River from a preparation plant located in the Lick Creek drainage near St. Paul, VA.	S.A. Ahlstedt (pers. obs.)
1978	Black-water releases from a settling pond into the Powell River from a preparation plant at Big Stone Gap, VA. Discharged water was thought to have affected ~200 river kilometers.	Carriker (1981), S.A. Ahlstedt (pers. obs.)
1982–1986	A Powell River mussel die-off is recorded, but its cause is unknown.	Ahlstedt and Jenkinson (1987)
1983–1988	Record low flows are caused by a prolonged drought in the Clinch and Powell rivers.	Ahlstedt and Tuberville (1997)
1983	A deep-mine blowout occurs on Bull Run Creek, a Clinch River tributary near Carfax, VA, creating a large slug of muddy water entering the Clinch River.	S.A. Ahlstedt (pers. obs.)
1986–1988	A Clinch River mussel die-off is observed, but its cause is unknown.	S.A. Ahlstedt (pers. obs.)
1992	Sediment toxicity to juvenile mussels is documented on the VA side of the Clinch and Powell rivers.	Olem (1980), McCann and Neves (1992)
1991–2004	Biological health of fish and macroinvertebrates are generally poor in tributary streams in the Clinch and Powell river drainages based on Index of Biotic Integrity sampling.	Angermeir and Smogar (1993), O'Bara et al. (1994), Ahlstedt and Tuberville (1997)
1996	An accidental black-water spill occurs in the North Fork Powell River, a major tributary to the upper Powell River, St. Charles, VA.	B. Evans (USFWS, pers. comm.)
1998	A truck accidentally dumps a rubber processing chemical into the Clinch River at Cedar Bluff, VA, resulting in a ~10 river kilometer kill of mussels, snails, fishes, and benthic macroinvertebrates.	Jones et al. (2001), Schmerfeld (2006)
2001–2004	Mussels are observed dead with meat inside their shells in the Clinch River (e.g., <i>Amblema plicata, Fusconaia subrotunda</i>).	S.A. Ahlstedt (pers. obs.)
2002–2003	Six black-water release events are documented in the Clinch and Powell river drainages.	B. Evans (USFWS, pers. comm.)

 $\rm m^{-2};$ Appendix II). Only at Buchanan Ford and Fletcher Ford did density ever exceed 10 $\rm m^{-2},$ but decades ago in 1979 and 1983. By 2004, density ranged from 1.4 to 2.2 $\rm m^{-2}$ among sites, except at Buchanan Ford where it remained comparatively high at 8.0 $\rm m^{-2}.$ Declines were steep at other sites over 25 y, varying from 69% at McDowell Shoal to 88% at Fletcher Ford (Table 3; Appendix II).

Actinonaias pectorosa and A. ligamentina were also the co-dominant species in the Powell River, though their densities over the study averaged only 2.0 m⁻² and 1.6 m⁻² per sample, respectively (Appendix II). Medionidus conradicus, Fusconaia subrotunda, and Elliptio dilatata were next in abundance, but relatively uncommon, averaging <0.6 m⁻² per sample. Endangered species density declined over the 25 y at all sites, and specimens were nearly always uncommon or rare

(≤0.4 m⁻² per sample). Among these, only *Dromus dromas* and *Plethobasus cyphyus* were found at each site, while *Epioblasma capsaeformis*, *F. cuneolus*, and *Quadrula cylindrica strigillata* were not found in quadrats after 1983.

A total of 47 species are known from the Powell River, and we consider 37 species to be extant, including 15 of 19 federally endangered species (Table 1). Overall, 28 of the extant species in the river are imperiled, 4 of which the USFWS has been petitioned to list under the ESA. Two other petitioned species are considered extirpated in the river.

Threats

We documented >30 anthropogenic trends, activities, or explicit events that have likely affected the mussel fauna in the

study area since the late 1800s (Table 4). They range from general changes in land-use (e.g., widespread logging, coal extraction, railroad construction) and direct exploitation (e.g., pearling, harvest) to catastrophic site-specific incidents (e.g., toxic spills ca. 1970 and 1998 in the Clinch River, VA). Most perturbations are based on the literature or personal communications with agency personnel, while others include personal observations by the authors.

DISCUSSION

Overview of the Mussel Faunas

A total of 48 of 55 species recorded from the mainstem Clinch River upstream of Norris Reservoir are considered extant, representing a faunal loss of 13% (Table 1). Our total species richness relative to that recorded by Jones et al. (2014) was 39 to 38, who quantitatively observed all 38 species in TN and 26 species in VA during 2004–2009. They sampled at our six sites plus three more sites in VA and seven more sites in TN. Based on this combined sampling over 30 y, we consider Leptodea fragilis, Quadrula intermedia, and Villosa fabalis to be extirpated from the Clinch River, while Epioblasma haysiana, E. lenoir, and E. torulosa gubernaculum are now extinct. All six species likely persisted in the river until the early 1970s to mid-1980s. Though we did not detect Epioblasma florentina aureola during our sampling, we consider it extant in the upper Clinch River mainstem in VA, despite the catastrophic pollution spill in 1998 that killed at least 182 individuals of this critically endangered species (Jones et al. 2001; Schmerfeld 2006; Table 4). We also did not observe Toxolasma lividum—an FMCS vulnerable petitioned species not reported alive for decades—but consider it extant based on shells collected in TN since the mid-1990s (Jones et al. 2014), and it being a small and easily overlooked species that primarily occurs in seldom-sampled stream margins. Pleurobema sintoxia was considered extirpated (Jones et al. 2014), until fresh-dead shells collected from muskrat middens in Hancock County, TN, in 2013 confirmed its continued presence (S.A. Ahlstedt, unpub. data). It is possible that this species has been confused with individuals of P. cordatum or P. plenum over the past few decades.

Other Clinch River records need clarification. *Epioblasma stewardsonii* was reported erroneously from the Clinch River upstream of Norris Reservoir by Stansbery (1973) (and repeated by Jones et al. 2014) based on an Ortmann (1918) record actually reported from a pre-impoundment site. Though Ortmann (1918) reported both forms of *Quadrula cylindrica*—the headwater subspecies *Q. c. strigillata* and the nominate subspecies *Q. c. cylindrica* (as *Q. cylindrica*)—from the currently unimpounded upper Clinch River, we do not recognize the occurrence of the nominate subspecies in our study area. Our viewpoint is supported by Stansbery (1973) and USFWS (2004). We accept the federally endangered *Leptodea leptodon* as part of the study area mussel fauna based

on a museum specimen (U.S. National Museum 150158) with the stream of origin missing from the label (only "Scott County, Virginia" appears for a locality). In all likelihood the specimen is from Clinch River (Williams et al. 2008), which represents a new state record for VA. Probably collected in the early 1900s, the species is now extirpated from the study area. Jones et al. (2014) also recognized this specimen but their position was equivocal, stating that it may have been collected from either the Clinch River or North Fork Holston River. Lastly, recent mitochondrial DNA and soft anatomy data has shown that Villosa perpurpurea and Villosa trabalis in the Clinch River are the same species, which makes the former taxon a synonym of the latter taxon based on priority (Lane et al. 2016). Further, these data show that the species actually belongs in the genus Venustaconcha (Kuehnl 2009; Lane et al. 2016). These taxonomic name changes are reflected in our paper accordingly.

A total of 37 of 47 species recorded from the mainstem Powell River upstream of Norris Reservoir are considered extant, representing a 21% faunal loss (Table 1). Johnson et al. (2012) stated that the Powell River had "likely lost one-third of its species" over the last century. Our estimate of decline reflects an optimistic view that several species may continue to exist but at abundance levels difficult to detect, especially by quadrat sampling. For example, Strophitus undulatus was rediscovered in 2013 in Claiborne Co., TN, after a nearly 40-y absence from collections (T. Lane, Virginia Tech, unpub. data). Regardless, based on Johnson et al. (2012) and our study, we consider Lasmigona holstonia, Leptodea fragilis, Pegias fabula, Toxolasma lividum, and Venustaconcha trabalis to be extirpated from the Powell River, and Epioblasma haysiana, E. lenoir, and E. torulosa gubernaculum to be extinct (Table 1). Of note, while L. holstonia likely is extirpated from the mainstem, it still occurs in at least one headwater tributary, South Fork Powell, VA (R.S. Butler, unpub. data). With the exception of L. fragilis (observed only in 1979), most of these species had likely disappeared by the 1960s. Two additional species, Epioblasma lewisii and Villosa fabalis, occurred in the Powell River a century ago (Ortmann 1918), but were reported only from sites inundated by Norris Reservoir. Herein, we report *Cyprogenia stegaria* for the first time from the Powell River, based on collections made several decades ago at McDowell Shoal but overlooked in previous studies (S.A. Ahlstedt, unpub. data). No additional records of this species are known, indicating that it is likely extirpated from the river.

Another record warrants discussion. We also include *Anodontoides ferussacianus* in Table 1 based on a record in Ortmann (1918) of two specimens from an unspecified site on Powell River, Lee County, VA, likely collected well over a century ago. Ortmann (1918) considered the record to be unequivocal, indicating he must have personally studied the specimens. The Powell River record has subsequently been overlooked; the genus is not reported anywhere else in the Tennessee River drainage, and it represents another addition to the VA mussel fauna. Since *A. ferussacianus* is primarily a

smaller stream Midwestern species (Watters et al. 2009) with a range well over a thousand river kilometers from the study area, the form from the Powell River is unlikely the same species. The specimens may actually represent *A. denigrata* from the adjacent upper Cumberland River drainage (located across the drainage divide in Kentucky), or possibly an undescribed species of *Anodontoides*.

Among the 24 federally listed species historically known upstream of Norris Reservoir in the Clinch River, 19 of them were shared with the Powell River; 20 and 15 listed species, respectively, are considered extant (Table 1). Endangered species now comprise 40–50% of the Clinch and Powell River mussel faunas. Such high levels of endangered species richness are unparalleled among diverse freshwater faunas of North America. The similarity of endangered species richness over time suggests that declines in the two rivers documented over the past century have been roughly parallel, having affected their faunas to similar degrees, though overall species losses are higher in the Powell River (21% vs. 13%; Table 1). About three-quarters of the extant fauna in these rivers are now comprised of imperiled species.

Clinch River Mussel Declines in VA

The decline in mussel density among Clinch River, VA, sites was highly significant over the study period, and species richness also decreased (Table 3; Figure 2B; Appendix I). Precipitous declines by more than 90% were observed at Pendleton Island (highly significant; Figure 2C) and at Semones Island (untested). These two sites occur in the lower half of a 68-km reach considered a "dead-zone" due to a severe decline in mussel density over more than a 30-y period (Jones et al. 2014). Further, if the 2009 data observed at the three VA sites by Jones et al. (2014) are included in the GLM analysis (1979–2009), the declining trend in mussel density over time remains highly statistically significant (J.W. Jones, unpub. data).

The density decline at Pendleton Island observed during our study continues (Figure 2C); sampling in 2009 produced a density of only 0.7 m⁻², dropping from 4.6 m⁻² in 2004 (Jones et al. 2014). The decline of the mussel fauna at this site is notable for several reasons. In the 1970s the site harbored 46 species, making it arguably the most diverse site in the country at the time (Jones et al. 2014). In 1979, mussel density was second only to Kyles Ford. Species that were once common are now rare (e.g., Actinonaias spp., Cyclonaias tuberculata, Fusconaia subrotunda, Lampsilis ovata). Many of the remaining species are relatively long-lived, and several short-lived species are already extirpated, an indication of recruitment failure. We recorded the short-lived (\sim 5 y; Haag 2012) Leptodea fragilis at Pendleton Island in 1979 but nowhere in the Clinch River since then, indicating that it is likely extirpated from the site and river.

Declines on the VA side of the Clinch River also were evident among endangered mussels. By 2004, endangered

species were very rare, extirpated, or existed at levels difficult to detect using standard quantitative sampling techniques. Three of six listed species we observed at Pendleton Island in 1979—Fusconaia cuneolus, Ptychobranchus subtentus, and Quadrula cylindrica strigillata—were common (1.1–1.3 m⁻²) at that time, but have not been observed in quantitative samples since 1999. Among listed mussels, only Fusconaia cor was sampled in 2004. The decline of Fusconaia cuneolus at this site is noteworthy, since it was the most common mussel (2.3 m⁻²) among the endangered species at the site during the 1970s and fourth in relative abundance, comprising 11.6% of the entire mussel assemblage (Dennis 1989). The last record of Quadrula intermedia in the Clinch River was a fresh dead shell at Pendleton Island in 1983 (Ahlstedt 1991a). Further, Epioblasma torulosa gubernaculum was also last observed at this site in 1983 (Jones et al. 2014) and at Kyles Ford during 1973-1975 sampling (Dennis 1985). The Clinch River, VA, also was the final refugium for E. haysiana, last collected as shells in 1970 (R. Muir, U.S. Geological Survey [USGS] retired, pers. comm.) and in 1984 near Cleveland, VA (R.J. Neves, USGS retired, pers. comm.), and one of the last refugia for E. lenoir, last collected as a shell in the 1960s near St. Paul, VA (Haag 2009).

Speers Ferry had the best mussel fauna among VA sites that we studied. Though the mussel assemblage at this site occurs at a moderate density (>3.7 m⁻² since 1999), recruitment is evident and density appears to be increasing, last recorded at 5.0 m⁻² in 2009 (Jones et al. 2014). Medionidus conradicus was the most common species and the only mussel with a density $>1.0 \text{ m}^{-2}$ since 1999. Despite its abundance, this Tennessee-Cumberland province regional endemic species is considered threatened by FMCS and is petitioned for federal listing. The federally endangered Epioblasma brevidens and Ptychobranchus subtentus appear to be increasing in density in recent years, as have Elliptio dilatata and Lampsilis fasciola, though densities for all four species remain low ($<0.6 \text{ m}^{-2}$ since 1999). In contrast, the endangered Venustaconcha trabalis was last sampled there in 1988 and now is rare in the upper river mainstem.

Improvement of the Mussel Fauna in the Clinch River, TN

Mean mussel density increased significantly at TN sites in the Clinch River from 1979–2004 (Figure 2A). Several species account for most of the general increase, particularly *Actinonaias pectorosa*, *Medionidus conradicus*, and *Ptychobranchus subtentus*, but also *Lampsilis fasciola*, *P. fasciolaris*, and the FMCS endangered and petitioned for listing *Fusconaia subrotunda*. The latter species is now common (1.4 and 1.7 m⁻²) at Brooks Island and Kyles Ford, respectively (Appendix I); Clinch River likely represents its largest population rangewide. Densities of some of the rarer endangered species have generally increased, such as *Cyprogenia stegaria*, *Dromus dromas*, *Epioblasma capsaeformis*, and *Epioblasma brevidens*. *Pleurobema rubrum*, an FMCS endangered species that also has

been petitioned for listing, was not detected during our study. Nevertheless, it remains a rare species in the Clinch River, which represents one of its largest population's rangewide. Several other species have maintained relatively stable abundance levels since 1979, namely *A. ligamentina, Cyclonaias tuberculata*, and *Lampsilis ovata*, or have occurred at low densities (<0.5 m⁻²) and were sporadically observed during our study, such as *Lasmigona costata* and *Amblema plicata*.

The population of *Epioblasma capsaeformis* in the Clinch River has varied tremendously since the 1970s, highlighting how population trends differ within species over time. The species was common during 1973-1975 sampling, representing 34.0% of mussel abundance at Speers Ferry and 17.7% at Kyles Ford (Dennis 1985, 1989). It declined over the next decade and by 1987, Dennis (1987) warned that E. capsaeformis had become "all but extirpated from Speers Ferry and Kyles Ford." The species remained generally uncommon in the river through the early 1990s while disappearing from several other rivers (e.g., Powell River), prompting its listing as endangered in 1997. Our data show that its population then began to increase appreciably by 2004. By 2009, E. capsaeformis became the second most abundant mussel on the TN side of the Clinch River (Jones et al. 2014), even exceeding abundance levels observed in the mid-1970s. The decline of this and other mussel populations in the mid-1980s may have been initiated by combined effects of a prolonged drought and chronic pollution (Ahlstedt and Tuberville 1997). Environmental conditions may have remained sub-optimal until ca. 1999 when favorable conditions allowed the species to recover ($>1.0 \text{ m}^{-2}$).

The TN section of the Clinch River is not without some species losses and declines in density. Notably, *Leptodea fragilis* and *Quadrula intermedia* likely were extirpated from this reach by the mid-1970s. Though not collected in our quantitative sampling since 1979, *Truncilla truncata* was collected from the TN reach during quantitative sampling in 2005 (Jones et al. 2014). The species has either declined drastically since being relatively common circa 1980, or it may survive in habitats infrequently sampled, such as in pools (Ahlstedt 1991a). Species richness, number of listed species, and density at the three TN sites reached their lowest levels in 1988, which was attributed to summer drought conditions from 1983 to 1988 (Ahlstedt and Tuberville 1997).

Decline of the Powell River Mussel Fauna in TN and VA

The downward trend in mussel diversity and abundance in the Powell River has been evident for decades. A century ago, Ortmann (1918) reported the headwater sites in VA to be depauperate, noting that even common species were often absent. Surveys in the 1970s yielded 36–37 species (Ahlstedt and Brown 1979; Dennis 1981; Ahlstedt 1991b), while another study during 1988–1989 recorded 28 species (Wolcott and Neves 1994). The 1970s surveys yielded no mussels at sites in the uppermost Powell River where Ortmann (1918) reported 13

species. Ortmann (1918) reported several imperiled species now considered extirpated from the mainstem (e.g., Lasmigona holstonia, Pegias fabula, Toxolasma lividum, Venustaconcha trabalis; Table 1). Further, if the 2009 data collected from the three TN sites and one VA site by Johnson et al. (2012) are included in the GLM analysis (1979–2009), the declining trend in mussel density over time remains highly statistically significant (J.W. Jones, unpub. data). Collectively, we found 26 species in 1979, but only 14 in 2004 (Appendix II). The trend continues, as is evident in the significant decline in density over our study period (Figure 2D). Mussel density at Buchanan Ford fared better than our other three sites where declines were steep (Table 3; Appendix II).

Species once common in the Powell River have become increasingly rare, including Actinonaias spp. and Medionidus conradicus. Fusconaia subrotunda was once one of the more common and widespread mussels in the river, but it was not collected after 1994 (Appendix II). No species other than these four occurred at densities of >1.0 m⁻² during our sampling regime. Lack of recruitment of these common mussels was noted in the late 1980s (Wolcott and Neves 1994). The FMCS vulnerable Pleuronaia barnesiana, a regional endemic and petitioned species, was also one of the most common species in the 1970s (Dennis 1985), but we found no evidence of it after 1983. Both F. subrotunda and P. barnesiana persist in the river but are rare (Johnson et al. 2012). Quadrula pustulosa is a common, widespread species not detected during our survey; it persists as the rarest of four Quadrula species, and ironically the only one that is not endangered (Johnson et al. 2012; Table 1). Another common species, Strophitus undulatus had not been reported from the river since the 1970s (Ahlstedt and Brown 1979; Dennis 1981) until found in 2013 in TN. Other common and widespread species, including Alasmidonta marginata and Leptodea fragilis, were not observed after 1979, while Truncilla truncata went undetected during our study. Though all three species were considered likely extirpated from the Powell River by Johnson et al. (2012), we believe A. marginata may persist. It is substantially longer-lived than L. fragilis (Watters et al. 2009) indicating that its extirpation would take longer to detect. Similarly, S. undulatus is very sporadic and has been perpetually rare in study area collections. We observed Pleurobema oviforme—a once common but now FMCS threatened regional endemic and petitioned species—only in 1979 and 1988 at Fletcher Ford. The species may persist but essentially at undetectable levels (Johnson et al. 2012).

Federally endangered mussels in the Powell River were always sporadic in occurrence in our quadrat samples, with no single species ever exceeding 0.6 m⁻². *Dromus dromas*, *Epioblasma brevidens*, and *Plethobasus cyphyus* represented the most frequently encountered endangered species in our study. We did not observe *Hemistena lata*, *Cumberlandia monodonta*, and *Lemiox rimosus*, though Ahlstedt and Brown (1979) and Dennis (1981) reported these species from three of our sites prior to 1979; recent data suggests that they remain in the river. A relatively fresh dead specimen of the deeply-

buried, easily overlooked *H. lata* was collected at Bales Ford in 1999 (J.W. Jones, unpub. data). A fresh dead specimen of C. monodonta was found during 2008-2009 (Johnson et al. 2012). This species usually occurs under large slab boulders (Stansbery 1967), a habitat type not well represented during our sampling. Lastly, 15 live individuals of *L. rimosus* were observed at five sites during 2008–2009 (Johnson et al. 2012). We did not observe E. capsaeformis after 1983, and the species was last reported in the river during 1988-1989 sampling upstream of our VA site (Wolcott and Neves 1994). Considered extirpated, it is now being reintroduced to multiple sites in TN and VA (Carey 2013). Quadrula cylindrica strigillata, Q. intermedia, and Q. sparsa were observed sporadically during our study. The population of Q. sparsa in the Powell River represents the only recruiting population known, underscoring its conservation importance. The other five endangered species considered extant—E. triquetra, Fusconaia cor, F. cuneolus, Pleuronaia dolabelloides, and Ptychobranchus subtentus—are very rare in the Powell River (Johnson et al. 2012).

Similar to the upper Clinch River, VA, mussel declines in the Powell River appear to have been driven by anthropogenic perturbations (Table 4). Change in the mussel fauna at McDowell Shoal epitomizes this decline in diversity and abundance. In the mid-1970s, 38 species were reported there, clearly making it the most productive site known in the river (Ahlstedt and Brown 1979, Dennis 1981; Ahlstedt 1991b; S.A. Ahlstedt, unpub. data). A mussel die-off lasting about three years, was reported by Ahlstedt and Jenkinson (1987) while conducting our 1983 sampling regime at this site; it was postulated that a toxic spill could have been the cause (Ahlstedt and Tuberville 1997). Ahlstedt and Jenkinson (1987) noted significant declines of the dominant species at the site, Actinonaias ligamentina, and total mussels sampled in quadrats between 1979 and 1983. Our data indicate that A. ligamentina never again achieved earlier densities. Collectively, we recorded 22 species in quadrats since 1979, but only 15 species since 1994 and 7 species in 2004. Though 17 species were recorded by Johnson et al. (2012) during qualitative sampling during 2008–2009, they found only 5 species in quadrats. Currently, several Powell River sites have higher species richness than McDowell Shoal. Fletcher Ford also has experienced a severe mussel decline since the late 1970s. In 1978, a density of 24.2 m⁻² was calculated for the site (Neves et al. 1980). We recorded steady declines since 1979, with density declining to 1.4 m⁻² by 2004.

Historical and Persistent Threats

European settlement of the Southern Appalachian Mountains brought with it vast changes to the landscape and its river drainages through logging, coal mining, railroads, and other activities (Eby 1923; Woodward 1936; Caudill 1963; Hibbard and Clutter 1990; Table 4). Riverine impacts and threats to the mussel fauna in the study area were documented a century

ago; Ortmann (1918) noted specific activities detrimental to mussels, such as a wood extraction facility in the upper Powell River drainage near Big Stone Gap, VA. The post-impoundment collections made by Stansbery (1973) in the Clinch River clearly reflected a decline in species distribution and richness over the previous half century. Both authors anticipated further declines in the fauna based on trends and their observations.

Numerous perturbations in the study area have resulted in catastrophic impacts to the mussel fauna (Table 4). Some dieoffs were directly attributable to chemical releases and spills (e.g., Cairns et al. 1971; Crossman 1973; Jones et al. 2001; Schmerfeld 2006), whereas others were less discernable (e.g., Ahlstedt and Jenkinson 1987; Jones et al. 2014). The decline of mussels in the Clinch River "dead zone" reach in VA, which includes Semones and Pendleton islands, likely was due to various poorly understood anthropogenic impacts over time (Krstolic et al. 2013; Johnson et al. 2014; Jones et al. 2014; Zipper et al. 2014). This faunal loss falls under the category of Haag's (2012) enigmatic declines, where all species are affected equally, and subsequent abundance of species postimpact is typically a function of pre-impact population size. The decline of the mussel fauna at Pendleton Islandespecially the extinction of E. torulosa gubernaculum represents one of the greatest losses to mussel conservation over the past 35 y. A long history of anthropogenic impacts to habitat quality in the Powell River has taken a similar toll on its fauna (McCann and Neves 1992; Wolcott and Neves 1994).

Natural resource exploitation has a long history in the Southern Appalachians and extraction of fossil fuels has often been implicated directly in mussel declines in the study area and elsewhere (Wolcott and Neves 1994; Ahlstedt and Tuberville 1997; Haag and Warren 2004; Warren and Haag 2005). The production of coal in VA peaked in 1990 and has since been in decline (Virginia Energy Patterns and Trends 2014). Coal mining and secondarily natural gas extraction nevertheless may pose the most significant threat, and spills from active and inactive coal processing waste ponds are common (Hampson et al. 2000; Table 4).

Impacts of coal mining on river fauna were reviewed by Hull et al. (2006). Mine-related pollutants that may impact mussels (e.g., water column ammonia, arsenic and other metals in sediments) were identified in the Clinch and Powell river drainages (Price et al. 2011). Though contaminants have declined in recent decades, total dissolved solids continue to rise in mined watersheds (Zipper et al. 2016). Research indicates that mussel populations were inversely correlated with deposited coal fines (Kitchel et al. 1981). Juvenile mussels tested in Powell River sediments sampled downstream of a coal processing facility had significantly lower survival rates (p = 0.01) than did juveniles tested in sediments from upstream of the facility (McCann and Neves 1992). Periodic heavy metal toxicity may have played a role in the mussel decline observed at McDowell Shoal in the mid-1980s (Ahlstedt and Jenkinson 1987; Ahlstedt and Tuberville 1997). In general, losses in mussel diversity and particularly abundance are greater on the VA side of the Powell River

(Johnson et al. 2012), though this is not apparent from data at our single VA site. The prevalence of resource extraction activities in the headwaters—first timber, then fossil fuels—may largely explain this continuing trend, first observed by Ortmann (1918). This phenomenon is mirrored in our data from the VA side of the Clinch River, and its cause may be similarly complex.

Stochasticity becomes an increasing threat to small, fragmented, and declining populations (Lande et al. 2003); many such mussel populations in the Clinch and Powell rivers are vulnerable to extirpation due to the absence of source populations for recolonization (Allendorf and Luikart 2007). Extinction debt models predict that in populations isolated by habitat destruction, even good competitors and abundant species are susceptible to eventual extirpation (Tilman et al. 1994; Hanski and Ovaskainen 2002). After the initial extinction of numerous mussel species in the early to mid-20th Century caused primarily by impoundments and secondarily water pollution in these rivers, a second extinction "wave" in the 21st Century may affect a broader suite of species due to effects from small population size and fragmentation (Haag 2009; Haag and Williams 2013).

Conservation and Population Restoration Efforts

Malacologists and resource managers in the region have written strategies to guide population restoration and conservation in streams like the Clinch and Powell rivers (Cumberlandian Region Mollusk Restoration Committee 2010; USFWS 2014). Culture facilities of the Virginia Department of Game and Inland Fisheries (VDGIF) and Virginia Tech have implemented a recovery program for increasing mussel diversity and abundance in these rivers. Various reintroduction methodologies have been attempted; translocation of adult mussels from large populations is the most cost-effective method for reestablishing historical populations, though density of available source populations is a limiting factor for most species (Carey et al. 2015). Researchers have refined culture methods for juveniles, allowing greater sizes for release and improved survival rates (Hua et al. 2015).

Epioblasma capsaeformis is the focus of concerted population restoration efforts in the upper Clinch River, VA, and Powell River, TN; survival has been high in both localities and evidence of recruitment documented in the Clinch River (Carey et al. 2015). Other endangered species that are being reintroduced or augmented include E. brevidens (Powell River, TN) and Lampsilis abrupta (Clinch River, TN and VA), in addition to several state priority species in VA in the Clinch River (VDGIF, unpub. data). The fortuitous abundance of Clinch River mussels in TN (e.g., E. brevidens, E. capsaeformis, Medionidus conradicus, Ptychobranchus subtentus) is serving as seed stock for most of these efforts and reintroductions elsewhere in the Tennessee River drainage (Hubbs 2016). Reestablishment of endangered species in historical river reaches

increases spatial distribution, improves overall conservation status, and represents the primary means by which recovery under the ESA can be achieved (USFWS 2004).

Fewer species have become extirpated in the Clinch and Powell Rivers compared to many other southeastern United States rivers, and most probably did so prior to 1994. There remains the potential to lose additional species in both watersheds through continued downward spiral of small populations of some species, but positive advancements in research, culture, population reintroduction, habitat restoration, and conservation are providing the knowledge necessary to prevent further declines and extirpations. These collective efforts offer tangible hope for the conservation of the extant fauna, and to create a malacological preserve for imperiled species in the Clinch and Powell rivers.

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Appendix I. Summary of mussel density in the Clinch River at six sites sampled in TN and VA during quantitative surveys conducted from 1979–2004. NA = data not available or collected.

	(CRKM 277.1)	(CRKM 277.1)	277.1)			(C)	(CRKM 295.8)	(8.5)			(CRK	(CRKM 305.1)			(C	(CRKM 339.7)	(2.6)) C	(CRKM 364.2)	4.2)		(CRK	(CRKM 378.4)	-
Scientific Name	1979 1988		1994 1999	2004	1979	1988	1994	1999	2004	1979	1988	1994	1999 2	2004	1979 1988	1994	1999 2004	04 1979	9 1988	1994	1999 20	2004 1983	1988 1994		1999 2004
(1) Actinonaias ligamentina	5.10 0.60	4.00	1.90	6.50	0 6.62	5.85	7.54	3.54	5.10	7.41	5.66	7.41	89.8	5.00	0.80 0.50	0.50	0.90 0.70	70 3.40	O NA	2.60	2.50 0	0.50 1.90	1.00	1.60 0.	0.70 0.10
(2) Actinonaias pectorosa	- 09.0	2.70	1.40	8.30	0.31	0.46	0.92	15.08	0.30	6.05	2.44	9.46 3	33.76 2	21.50 1	1.10 0.70	0 1.20	0.90 0.10	10 3.60	NA 0	3.40	4.30 1.80	80 2.50	1.80 1.90		1.60 0.80
(3) Alasmidonta marginata			•	0.10	-	1	,	,	,	,	0.10	0.10	,	,		•	1	'	NA		,		1	,	'
(4) Amblema plicata	- 0.10	0.10		1	0.15	1	,	0.46	,	0.39	0.29	,		,	- 0.10	-	1	0.80	NA 0	0.10	0.30 0	0.40 0.20	0.10	0.20	'
(5) Cumberlandia monodonta*	1		•	•	1	•	,		,	0.78	0.10	0.10		0.10	1	•	1	1	NA	1	,			,	'
(6) Cyclonaias tuberculata	- 0.10	0.10	0.60	0.10	1.08	3 1.08	0.62	,	0.90	0.39	0.29	0.39	0.20	0.30 0	0.20 0.10	-	0.40	1.10	O NA	0.50	0.70	0.60 0.20	0.30	0.50 0.	0.20
(7) Cyprogenia stegaria*	,	1	0.10	0.10	-	1	0.15		0.30	0.10	0.10	0.10	0.39	0.20	0.10 0.10	-	1	'	NA	•	ı	1			'
(8) Dromus dromas*	0.10 0.10	0.10	0.80	1.50	-	,	,	0.46	,	,	,	,	0.39	0.20	1	٠	1	1	NA	•	ı			,	
(9) Elliptio crassidens	1		•	•	1	1	0.15	0.31	,	,	,			0.50	1	•	1	1	NA	•	1			,	
(10) Elliptio dilatata	,		•	•	1	1	,	0.31	0.20	2.15	0.29	0.49	0.39	1.40 0	0.10 0.10	-	0.20 0.30	30 6.30	N O	1.40	0.80	0.20 0.10	0.10	0.10 0.	10 -
(11) Epioblasma brevidens*	- 0.20	0.30	0.60	09.0	-	0.31	0.31		1.10	0.10	,	0.29	0.88	0.30	- 0.10	-	0.60 0.30	- 08	NA	•	1	1			
(12) Epioblasma capsaeformis*	1	0.10	1.00	0.00	-	1	0.62	4.46	2.60	0.39	0.10	89.0	2.54	2.10 0	0.20	1	- 0.20	20 0.80	NA 0	1	ı	- 0.10	1	,	1
(13) Epioblasma triquetra*	0.10	0.10	0.10	1	0.15	1	0.31	0.31	0.90	0.10	,	,	0.10	0.10	1	•	,	'	NA	•	,	1	,	,	'
(14) Fusconaia cor**	,	1	,	•	1	1	,	,	,	0.20	,	,	,	,	1	•	- 0.10	10 0.30	N O	0.40	- 0	0.20 0.30	1	0.10	'
(15) Fusconaia cuneolus*	,	1	,	1	'	1	,	,	0.20	0.29	0.39	0.20	1	0.20	- 0.10	-	1	1.10	O NA	0.30	0.70	1	0.20	0.10 0.	0.20
(16) Fusconaia subrotunda	0.30	1	0.10	0.20	0.46	0.62	0.77	0.62	1.40	0.78	0.29	1.17	1.56	1.70 0	0.10 0.10	-	1	1.70	0 NA	2.00	1.90	0.10 1.00	0.70	1.70 0.	0.20 0.20
(17) Hemistena lata*	0.10	0.30	0.10	09.0	0.15	1	0.15	0.15	,	0.10	0.20	0.20	0.20	0.10	1	1	1	'	NA	,	,	1	1	1	'
(18) Lampsilis fasciola	,	0.20	0.30	0.50	'	0.15	0.15	0.31	09.0	0.20	,	0.10	0.49	0.70	1	0.10	0.20 0.30	30 0.20	NA 0	0.10	0.30	- 0.30	,	,	- 0.20
(19) Lampsilis ovata	$0.20 \ 0.10$		0.10	0.10	0.92	0.15	,	0.15	0.90	0.10	,	0.10	0.10	0.10	0.30 0.10	-	1	0.50	NA 0	•	- 0	0.10 0.10		- 0.	0.10
(20) Lasmigona costata	0.20 0.20	0.20	•	0.20	'	0.46	·	0.15	0.20	1.27	0.29	i	0.10	0.10	$0.20 \ 0.20$	0.10	1	1.30	NA O	0.10	0.20	- 0.10	0.10	0.20 0.	0.10
(21) Lemiox rimosus*	1	1	•	•	1	1	,	,	,	0.10	0.10	0.10	0.20	0.30	1	•	1	1	NA	•	1			,	1
(22) Leptodea fragilis		1	,	1	•	1	,	,	,	,	,	,	,	,	1	1	1	0.10	O NA	•	1	1	,	,	'
(23) Ligumia recta	- 0.10		0.10	•	0.31	1									1	•	1	0.10		•	,	1			
(24) Medionidus conradicus	0.10	1.00	2.00	2.20	'	1	0.46	5.69	0.50	2.44	2.24	10.34 2	22.15 2	20.10	- 0.40	0.50	1.30 1.30	30 0.20	NA 0	•	0.10			,	'
(25) Plethobasus cyphyus*	- 0.10	•	•	•	0.15	0.15	,		,	,	,	,	,	,		•	1	1	Z	•	ı			,	
(26) Pleurobema cordatum	,	ı	•	•	0.15	1	,	0.15	,	,		,			1	•	1	'	NA	•	ı			,	'
(27) Pleurobema oviforme			•	•	1	•	,	,	0.20	0.29	,	,	,	,		•	1	1	Z	•	,			,	1
(28) Pleurobema plenum*			•	•	1				0.00		ı				1	•	1	1	NA	1		1			1
(29) Pleurobema rubrum		1	•	•	1	1			,		,				1	•	1	1		0.10				,	1
(30) Pleuronaia barnesiana	0.10	0.10		0.10	-	•	,		0.20	2.15	,			,	1	0.10	1	0.10		•	,	- 0.10		,	1
(31) Pleuronaia dolabelloides*		1	,	1	•	1	,	,	,	,	,	,	,	,	1	1	1	'	NA	•	1	1	0.10	,	'
(32) Potamilus alatus	1	0.10		•	0.31	1	,		,	,	1	,		,	1	•	1	0.10	O NA	1	,	- 0.10		,	'
(33) Ptychobranchus fasciolaris	1	0.30	09.0	1.30	0.15	1	0.15		1.20	0.29	0.20	0.29	1.56	2.10 0	0.10	•	0.10 0.10	10 0.40	O NA	0.10	0.30 0	0.30 0.70	0.10	.10 1.	00 0.3
(34) Ptychobranchus subtentus*	0.10	0.80	1.60	6.10	0.15	0.46	1.08	8.62	3.40	4.20	0.59	5.56 2	20.29	16.20 0	0.50	0.10	0.20 0.30	30 1.10	O NA	0.10	0.10	1	0.10	,	- 0.1
(35) Quadrula cylindrica strigillata*		•	•	٠	٠	1			,	0.10			0.20	0.20	1	0.10	1	1.30	NA 0	٠	,	1		,	'
(36) Quadrula pustulosa	1	•	•	٠	0.31	1	0.31	,	,	0.10	0.29	0.10	0.10		1	٠	1	1	NA	٠	1			,	
(37) Strophitus undulatus	1		•	•	1		,		,		1				1	•	1	1	NA	1	,	1			
(38) Truncilla truncata			•	•	1	•	·	,	,	0.10	,	,	,	,	1	•	1	1	NA	•		1		,	1
(39) Venustaconcha trabalis*		•	•	•	1	•	·		,	i	i	i	,	,	- 0.10	-	1	0.10	O NA	•	,			,	
(40) Villosa iris			•	•	1	•	,	,	0.20	0.39	0.10	0.39	0.59	0.80	1	0.10	1	1	NA	•	0.20	- 04		,	1
(41) Villosa vanuxemensis	•	0.10	1	1	1	,	1	,	,	,	,	,	0.10	,	1	0.10		1	NA	,	,		,	1	1

*Federally endangered species and dash mark "-" = 0.

Appendix II. Summary of mussel density in the Powell River at four sites sampled in TN and VA during quantitative surveys conducted from 1979–2004.

£		(P.	(PRKM 159.5)	159.5)				(PR	(PRKM 171.7)	(PRKM 171.7)				(PRK)	(PRKM 179.9)				D	(PRKM 188.8)	188.8)	,	
Scientific Name	1979	1983	1988	1994	1999	2004 1	1979 19	1983 19	1988 19	1994 1999	99 2004	4 1979	1983	1988	1994	1999	2004	1979	1983	1988	1994	1999	2004
(1) Actinonaias ligamentina	5.50	6.30	1.20		0.90	2.10 2	2.40 0.3	0.80 0.5	0.50 0.6	0.60 0.50	0.40	0 1.80	3.00	0.20	1.20	1.40	0.80	1.90	1.24	0.76	2.10	1.24	0.19
(2) Actinonaias pectorosa	1.60	10.10	1.00	2.70	2.90	3.40 1	1.00 0.1	0.80	0.10 0.2	0.20 0.90	0.30	0 1.60	0.40	09.0	0.80	1.40	0.20	4.86	4.38	2.67	2.76	2.38	0.57
(3) Alasmidonta marginata	0.10	ı	ı	1	1	,	1				1	1	1	1	1	1	1	1	1	1	ı	1	1
(4) Amblema plicata	0.20	ı	ı	0.10	1	0.20	0.30 0.3	0.20 0.6	0.60 0.3	0.30 0.10	0.20	- (1	1	1	0.20	ı	0.10	1	0.10	0.19	1	ı
(5) Cyclonaias tuberculata	0.10	ı	0.10	0.10	'	0.10	1	,	0.	0.10 0.40	- 01	0.20	1	1	1	ı	ı	0.10	ı	0.10	0.19	0.19	0.19
(6) Dromus dromas*	ı	0.10	1	,	0.10	0.10	0.10 0.	0.10		1	0.10	0.20	1	0.20	0.20	0.20	1	1	1	1	ı	0.10	1
(7) Elliptio crassidens	0.20	,	1	1	1	0 -	0.20 0.	0.10 0.	0.10	'	1	1	1	1	1	1	ı	,	0.10	1	ı	1	1
(8) Elliptio dilatata	ı	,	1	1	'	0.20	0.10 0.	0.10 0.5	0.50 0.20	- 02	0.10	0.20	1	0.20	0.20	0.20	0.40	0.48	1.33	0.38	0.38	0.48	0.10
(9) Epioblasma brevidens*	ı	,	1	1	1	0 -	0.10	0.	0.10		1	1	0.20	0.20	1	1	ı	0.38	1	1	0.10	1	0.10
(10) Epioblasma capsaeformis*	0.30	,	1	1	ı		1	,			1	0.40	1	1	1	1	ı	0.29	0.19	1	ı	1	ı
(11) Epioblasma triquetra*	ı	0.30	1	1	1	,	1	.0	0.10		1	1	1	1	1	1	ı	0.10	0.10	0.10	ı	0.10	1
(12) Fusconaia cor*	ı	ı	ı	0.10	1	0 -	01.0	,			ı	0.20	1	1	1	ı	ı	,	ı	ı	ı	1	1
(13) Fusconaia cuneolus*	ı	0.10	ı	,	,	1	1	,			1	1	1	1	1	ı	ı	ı	ı	ı	1	1	1
(14) Fusconaia subrotunda	1.00	1.40	0.30	,	,	0 -	0.10 0.	0.10 0.3	0.30 0.1	0.10	1	1	0.20	0.60	'	ı	ı	0.38	0.95	0.38	0.86	1	1
(15) Lampsilis fasciola	ı	0.50	ı	0.10	'	0.40 0	0.20	,	1	0.10	- 0	1	0.20	0.20	0.20	1	0.20	0.38	0.29	1	1	0.10	1
(16) Lampsilis ovata	0.20	0.20	0.10	ı	0.10	0.10 0	0.20	- 0.	0.10	0.10	0.10	0.20	'	1	0.20	ı	ı	,	0.10	ı	ı	1	ı
(17) Lasmigona costata	0.20	0.10	ı	ı	0.10	0.10	ı			0.10	- 0	1	ı	1	1	0.20	ı	ı	0.19	ı	ı	ı	ı
(18) Leptodea fragilis	ı	ı	ı	ı	ı	ı	1	,			1	1	1	1	1	ı	ı	0.19	ı	ı	ı	1	1
(19) Ligumia recta	ı	0.10	ı	,	,	ı	1				1	•	1	1	•	ı	ı	1	ı	ı	1	ı	ı
(20) Medionidus conradicus	1.00	2.10	09.0	0.30	06.0	1.00 0	0.20	- 0	0.30 0.20	20 0.30	- 0	0.80	0.40	0.40	0.80	0.20	0.40	1.43	1.14	0.76	0.19	0.57	0.10
(21) Plethobasus cyphyus*	0.10	0.10	ı	ı	ı	- 0	0.10				1	1	0.20	'	0.40	ı	0.20		ı	ı	0.10	ı	1
(22) Pleurobema oviforme	1	ı	ı	,	,	,	1				1	1	1	1	1	1	ı	0.19	1	0.10	ı	1	1
(23) Pleuronaia barnesiana	ı	0.10	1	,			- 0.	. 10			1	0.80	1	1	1	1	1	0.19	0.10	1	1	1	1
(24) Pleuronaia dolabelloides*	ı	ı	ı	ı	ı	,	1		0.	0.10	1	1	1	1	1	ı	ı	ı	1	ı	ı	ı	ı
(25) Potamilus alatus	0.30	ı	ı	,	,	ı	1	,	'		1	•	1	1	1	ı	ı	ı	ı	ı	ı	•	ı
(26) Ptychobranchus fasciolaris	0.10	0.20	0.20	0.20	'	0.30 0	0.10 0.	0.10 0.	0.10	0.20	- 03	0.20	0.20	1	1	0.20	ı	0.10	0.10	0.10	0.10	1	0.10
(27) Ptychobranchus subtentus*	ı	ı	ı	0.10	1	ı	1	,			1	09.0	1	1	0.20	ı	ı	,	0.10	ı	1	1	1
(28) Quadrula cylindrica strigillata*	ı	ı	ı	ı	,	0 -	01.0				1	1	1	1	1	ı	ı	ı	ı	ı	ı	1	1
(29) Quadrula intermedia*	ı	0.10	ı	ı	0.10	0 -	0.20 0.	0.10 0.4	0.40	0.10	- 0	1	1	1	1	ı	ı	0.10	ı	ı	ı	1	1
(30) Quadrula sparsa*	1		1	ı	ı		1				1	1	1	1	0.20	0.20	ı		1	0.10	ı	1	1
(31) Villosa iris	1	ı	ı	,	,	,	1	- 0.	01.0		0.20	- (1	1	1	1	ı	1	1	1	ı	1	1
(32) Villosa vanuxemensis	ı	ı	ı	,	,	,	1	,			1	1	1	1	ı	1	1	ı	ı	1	1	ı	1
Total per meter squared	10.90	21.80	3.50	5.50	5.10 8	8.00 5	.50 2.	2.50 3.3	3.30 1.8	1.80 2.80	30 1.40	0 7.20	4.80	2.60	4.40	4.20	2.20	11.17	10.31	5.55	6.97	5.16	1.35

*Federally endangered species and dash mark "-" = 0.