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REGULAR ARTICLE

COLLAPSE OF THE PENDLETON ISLAND MUSSEL FAUNA IN THE CLINCH RIVER, VIRGINIA: SETTING BASELINE CONDITIONS TO GUIDE RECOVERY AND RESTORATION

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ABSTRACT

In the 20th century, Pendleton Island (PI) in the Clinch River of southwestern Virginia was a singularly important location for conservation of freshwater mussels in North America, supporting at least 45 species. Comprising 55,500 m^2 of available habitat, PI is the largest contiguous patch of habitat for mussels in the unregulated reaches of the Clinch River in either Virginia or Tennessee. Mussel density at PI declined by 96% from its historical baseline of 25/m^2 in 1979 to ~1/m^2 in 2014, indicating a collapse of the fauna. We provide a quantitative description of the PI mussel assemblage collapse and establish baseline conditions for restoration scenarios. We examined long-term monitoring data collected at 15 sites in the Tennessee and Virginia sections of the river over a 35-yr period (1979–2014). While the mussel assemblage of PI has declined precipitously, density in the Tennessee section of the river has increased at an annual rate of 2.3% (1979–2004) and 1.3% (2004–14), stabilizing at a mean density of 29/m^2 over the last 10-yr period, a reasonable baseline density to gauge recovery and restoration at PI and at other disturbed sites in the river. Lost mussel abundance can and should be translated to ecosystem services loss at PI, representing more than 1.38 million mussels and tens of millions of lost mussel service years. When density of the PI mussel assemblage is projected forward 30 yr (2014–44), it returns to a baseline of 25/m^2 in 2036 only under a high-growth-rate scenario of 15% per yr. If realistic growth rate scenarios of 1% and 5% are used, density reaches 1.4/m^2 (~75,000 individuals) and 4.3/m^2 (~240,000 individuals), respectively, by 2044. These scenarios assume healthy nondegraded habitat conditions, which do not reflect current water and sediment quality at PI. Recovery of the assemblage to baseline densities will take decades and require active restoration of the fauna and habitat, including mussel translocations and stocking of hatchery-propagated juveniles.

KEY WORDS: Clinch River, Pendleton Island, freshwater mussels, recovery, restoration

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INTRODUCTION

Pendleton Island (PI) in the Clinch River of southwestern Virginia persisted as a globally significant habitat for freshwater mussels into the late 20th century, with 45 species recorded since 1979. One of the most-speciose habitats in the Clinch River, PI supports among the greatest species richness remaining in North America (Jones et al. 2014; Ahlstedt et al. 2016); only Speers Ferry has comparable documented richness (Ostby and Beaty 2017). Further, it may have supported among the greatest number of species documented in a single habitat in North America since the 1960s, a period following a boom in construction of large hydro-power and flood-control dams throughout the Tennessee and Cumberland river systems. Historically, these river systems supported globally significant endemism and species richness. In the late 20th century, PI was identified as a conservation priority because it supported numerous rare and endangered mussel species, including 24 species listed as federally endangered. Consequently, PI was a priority for state and federal government agencies and The Nature Conservancy, which purchased it in 1986 to help manage and protect the mussel fauna.

First discovered by Tennessee Valley Authority (TVA) biologists Steven Ahlstedt and Charlie Saylor during a 1978 reconnaissance survey, PI was immediately recognized for harboring a large, abundant, and diverse mussel assemblage. The following year, the site was quantitatively surveyed, and a mussel density of $25/m^2$ was recorded (Ahlstedt et al. 2016). Unfortunately, the mussel assemblage has declined by 96% since then to its current density of $\sim 1/m^2$ (Jones et al. 2014). The causes of the decline include degraded water and sediment quality related to coal-mining activities occurring in the watershed for more than 50 yr, with data, analyses, and discussion available in Krstolic et al. (2013), Johnson et al. (2014), Price et al. (2014), Zipper et al. (2014), and Cope and Jones (2016). These authors present the current state of scientific understanding that water and sediment quality in this reach of the river are adversely affected by increased levels of contaminants, including dissolved solids, trace metals, and polycyclic aromatic hydrocarbons, which in turn may limit mussel survival and reproduction. While the faunal collapse has been clearly documented (Jones et al. 2014; Ahlstedt et al. 2016), the magnitude of lost mussel abundance, species richness, and ecosystem services at PI has not been well quantified, and baseline conditions have not been set to gauge future recovery and restoration of this important assemblage.

The comprehensive survey of the unregulated Clinch River conducted by TVA from 1978 to 1983 demonstrated that mussel density and richness are highly heterogenous. Habitat patches such as PI are mussel hotspots in a river that features predominately exposed bedrock dotted with cobble/gravel bars of limited extent and variable long-term stability. Church (1997) hypothesized that heterogeneity was a product of underlying lithology, geologic structure, and channel form. He found that two types of reaches were more likely to support "high-quality" mussel assemblages. The first mostly occurred when the Clinch River flowed in the direction of geologic dip over limestone or dolomite geology; there, bedrock outcrops oriented perpendicular to flow trapped alluvium, creating long-term stable habitats capable of supporting mussel beds. The second—of which PI was a specific example—occurred where the river flowed over comparatively erosive shale formations. In these reaches, valley floors were wide and the river tended to braid. With 55,500 m^2 of riverbed available, PI is by far the largest contiguous habitat patch for mussels in the unregulated reaches of the Clinch River in either Virginia or Tennessee. In fact, it contains a similar amount of habitat as the three largest habitat patches in the Tennessee section of the river combined; Wallen Bend (WB), Kyles Ford, and Frost Ford (FF) contain a total of 58,765 m^2 of habitat (Jones et al. 2014). PI's extent, however, is deceptive, because it cannot be viewed in its entirety from the ground due to the size of the island, length of the channels, and the tree canopy, which obscures the view. The site is located in Scott County, Virginia, at river kilometer (RKM) 364.2 (RKM 0 is at the confluence with the Tennessee River), in a faunal transition zone between the headwaters and lower half of the river (Fig. 1). The site contains two main channels, 800–900 m long, defined by the main island, but it also contains smaller channels defined by smaller islands. As a result, PI contains a diversity of small-scale niche habitats, including shallow riffles and long runs with gravel-sand substrates, areas with boulders and slab rock, and stretches with ample large woody debris, which collectively provide ideal habitat conditions for high species richness of mussels and their host fishes (Fig. 2). Further, species richness may result from PI's location in a stream network connecting isolated mountain headwaters to the broad rivers of the Tennessee Valley and the lower Mississippi River.

Survey data exist to establish baselines for mussel density, abundance, and assemblage structure at PI. Long-term monitoring data collected from 1979–2014 at multiple sites in Tennessee and Virginia by Jones et al. (2014), Ahlstedt et al. (2016), and this study provide a context to establish quantitative baseline conditions and prevent what has been described as the "Shifting Baseline Syndrome," in which "each generation of fisheries scientists accepts as a baseline the stock size and species composition that occurred at the beginning of their careers, and uses this to evaluate changes. When the next generation starts its career, the stocks at that time serve as a new baseline. The result obviously is a gradual shift of the baseline" (Pauly 1995, 430). Historically, changes to the mussel assemblage at PI and other sites in the Clinch River have occurred and will continue to occur in the future, driven by myriad ecological and anthropogenic factors as well as by stochasticity. Therefore, it is critical that future changes to the fauna are measured against quantitative and parameterized baseline metrics so that the next generation of biologists can accurately assess population trends for respective species at PI and throughout the river.

The broad purpose of this study was to build on quantitative data collected from 1979 to 2004 (Ahlstedt et al. 2016) and 2004 to 2009 (Jones et al. 2014) by continuing long-term monitoring from 2010 to 2014 at key sites in the

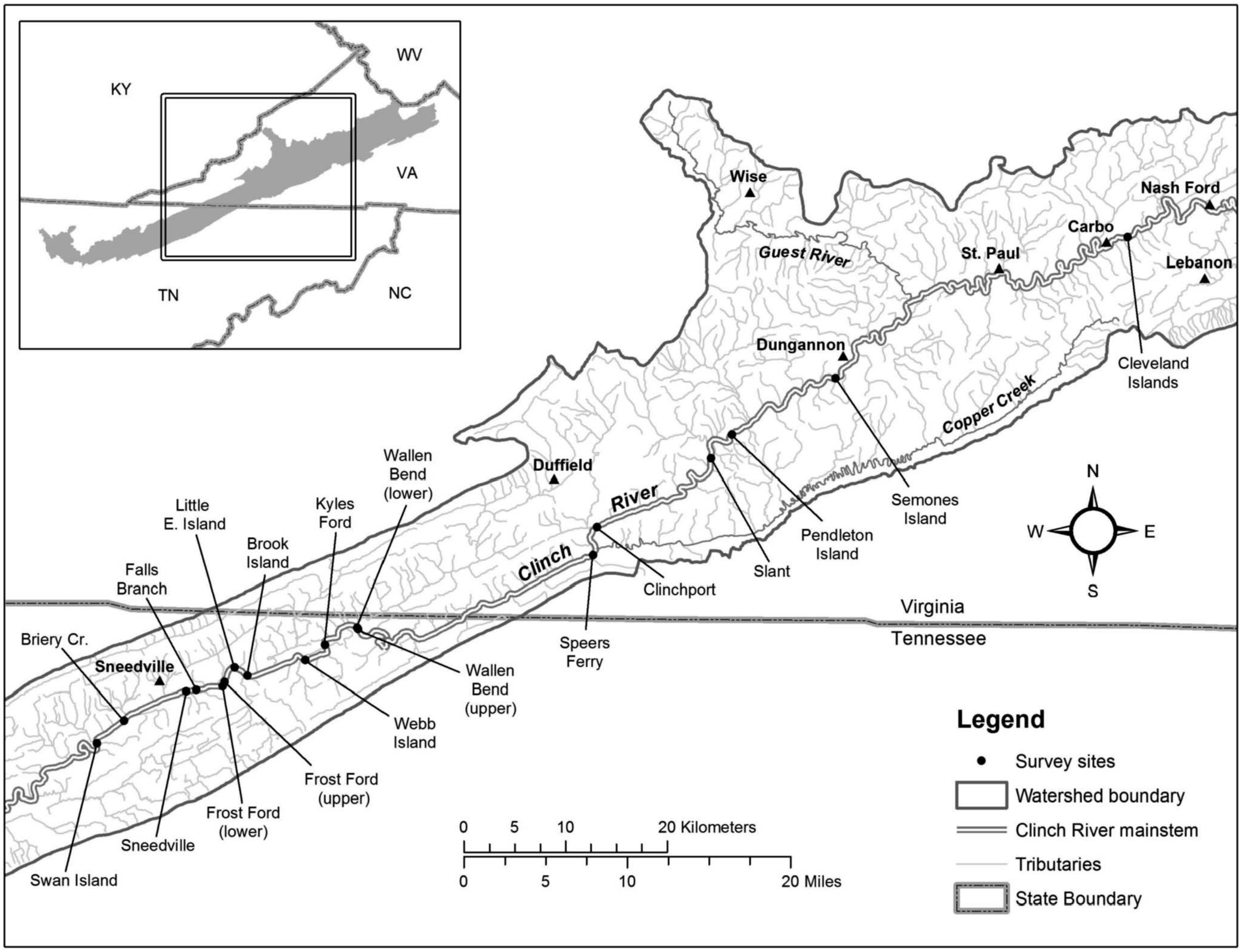

Figure 1. The 15 sites sampled during the study period from 1979 to 2014 in the Clinch River, Tennessee and Virginia, upstream of Norris Reservoir. Swan Island, upper Frost Ford, and upper Wallen Bend were sampled annually from 2004 to 2014, while remaining sites were sampled one to three times during the study period. Cleveland Islands, Slant, and Clinchport in Virginia were not sampled as part of the current study; data are available for these three sites in Jones et al. (2014), where the map was previously published.

Clinch River upstream of Norris Reservoir in Tennessee and Virginia, and to use the data to determine status and population trends of mussels throughout the river. More specifically, we used these data to set baseline conditions at PI for species composition and density so that recovery and restoration of the site's fauna can be accurately assessed in the future. Further, using four population growth rate scenarios to gauge recovery of the PI mussel assemblage in the future, we assessed lost mussel abundances, ecosystem services, and time to recovery over a 65-yr period (1979–2044).

METHODS

Establishing baseline conditions.—Two sections of the Clinch River made up the study area: (1) a 38.5-km section from Swan Island (RKM 271.1) upstream to Wallen Bend (RKM 309.6) in Hancock County, Tennessee, and (2) a 38.6-km section from Speers Ferry (RKM 339.7) upstream to Semones Island (RKM 378.3) in Scott County, Virginia, with a focus on the mussel fauna at PI (RKM 364.2) (Fig. 1). Since 1979, the mussel assemblage in the Tennessee section has been characterized by high abundance and assemblage stability, whereas the assemblage in the Virginia section has been characterized by low abundance and severe decline, including species extirpation (Jones et al. 2014). We analyzed mussel population densities at 12 sites in Tennessee and six sites in Virginia, which were initially surveyed from 2004 to 2009 (Jones et al. 2014), with a subset of those sites analyzed from 2010 to 2014 as part of the current study (Fig. 1 and Table 1). We did not sample three sites (Cleveland Islands, Slant, and Clinchport in Virginia) during the current study, but data and references are available for these sites in Jones et al. (2014). Hence, a total of 15 sites were sampled for the 2010–14 study period. Sites were sampled once or twice during the entire study period from 2004 to 2014, except for three

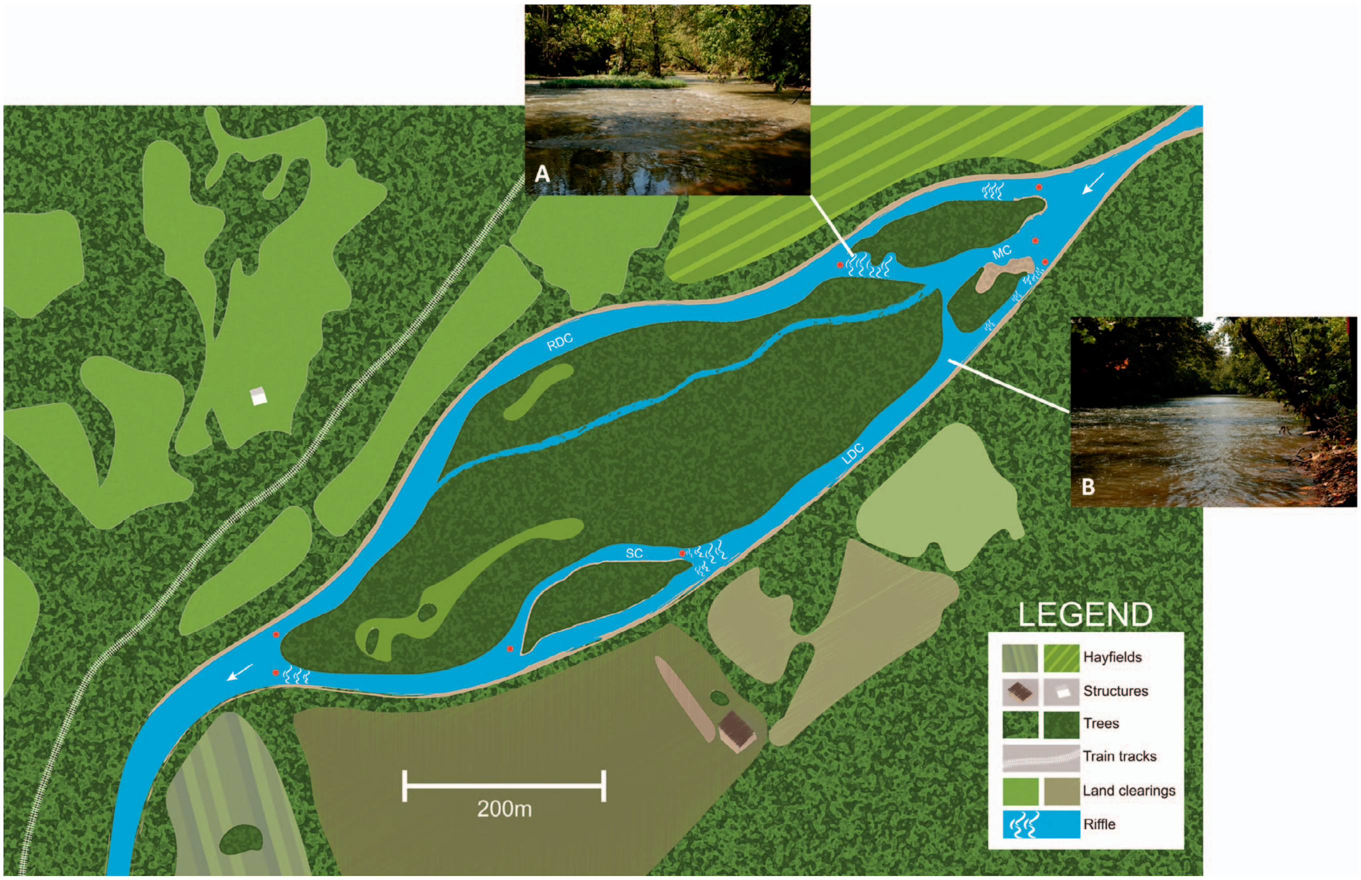

Figure 2. Graphic image of Pendleton Island, Clinch River, Scott County, Virginia showing right-descending channel (RDC), middle channel (MC), left-descending channel (LDC), side-channel (SC) of left-descending channel, and surrounding land features. RDC is 856 m long with mean width 25.7 m and LDC is 980 m long with mean width 24.9 m. Red dots indicate start and end points of the measured distance of each respective channel. Inset photograph A is a shallow riffle in RDC, and inset photograph B is a long run in LDC.

Tennessee sites, Wallen Bend (WB), Frost Ford (FF), and Swan Island (SI), which were sampled annually. These three sites were selected to establish and monitor baseline population trends in the Tennessee section of the river over the 10-yr period. To monitor population conditions in the Virginia section, Speers Ferry, Pendleton Island (PI), and Semones Island (SEI) were sampled in 2009 and then just PI and SEI in 2014. Most sites in Tennessee and Virginia also were sampled from 1979 to 2004 (Ahlstedt et al. 2016), and we combined those data with data from Jones et al. (2014) and the current study to analyze long-term population trends (1979–2014) in the Tennessee section of the river, and the long-term population trend at PI.

Because of the historical importance of the fauna at PI, we conducted additional analyses to establish and reconstruct baseline conditions for species density, abundance, and composition at the site using data from Jones et al. (2014), Ahlstedt et al. (2016), and the current study. In addition, we used data from several qualitative surveys conducted at PI to assess extant species richness at the site (Neves and Beaty 1996; Beaty and Neves 1997; Beaty and Neves 1998; Jones and Neves 1999; Ahlstedt et al. 2005). Historical mussel assemblage density for PI was set at $25/m^2$, the maximum observed density at the site as measured in 1979 (Ahlstedt et al. 2016). Each species' frequency, percentage composition of the assemblage (proportion), density, and abundance at the site was reconstructed by averaging species composition data from 1979 at PI with composition data from all sites in Tennessee from 2004 to 2014. Using *Actinonaias ligamentina* as an example to calculate baseline for a species, we calculate area of PI ($55{,}503\ m^2$) $\times$ baseline density ($25/m^2$) $\times$ mean proportion (0.10755) $=$ 149,234 individuals at the site (Table 5). It was necessary to use recent composition data from the Tennessee section of the river because many of the species known from PI were uncommon to rare even in 1979. Further, percentage compositions of the common species already were skewed toward longer-lived and more tolerant species. Hence, an averaging approach combining data from sites and time periods was required to reconstruct the most probable proportion of each species at PI. Finally, decline and recovery of the mussel assemblage from an historical baseline of $25/m^2$ was modeled first by linear regression of density data from 1979 to 2014 and then by projecting density over time from 2014 to 2044 using four growth rates—1%, 5%, 10%, and

Table 1. Site location, river kilometer, site area size, year sampled, sample size, and mussel density with 95% confidence intervals (CI) at sites sampled quantitatively with quadrats from 2004 to 2014 in the Clinch River, Tennessee and Virginia. The sample data are from [a]Ahlstedt et al. (2016), [b]Jones et al. (2014), and [c]Dennis (1989), and the current study includes data from 2010 to 2014. NA indicates that raw data were unavailable to calculate confidence intervals. *Quadrats were 0.5.

Site Location Name	River Kilometer (river mile)	Total Site Area (m^2)	Year(s) Sampled	No. (N) 0.25 m^2 Quadrats/yr	Mean Density/m^2	Lower 95% CI	Upper 95% CI
Swan Island (SI), Tennessee	277.1 (172.2)	5,760	1979[a]	40	7	NA	NA
			1988[a]	40	1.6	0.7	2.5
			1994[a]	40	10.6	NA	NA
			1999[a]	40	11.4	8.2	14.6
			2004[a]	40	29.4	22.2	36.6
			2004[b]	60	23.7	15.7	31.7
			2005[b]	60	15.1	8.8	21.4
			2006[b]	60	16.3	9.6	23
			2007[b]	60	22.5	16.4	28.6
			2008[b]	60	23.1	13.7	32.5
			2009[b]	72	28.2	20.6	35.8
			2010	80	27.5	20.5	36.9
			2011	80	26.7	19.9	35.9
			2012	80	34.2	25.4	46
			2013	80	17.7	12.6	25
			2014	80	15.7	11.5	21.4
Briery Creek, Tennessee	280.8 (174.5)	6,600	2006	40	12	8.9	15.1
Sneedville, Tennessee	287.6 (178.7)	2,016	2006	40	11.8	8.5	15
Falls Branch, Tennessee	288.7 (179.4)	5,334	2006	40	34.9	26.4	43.2
Frost Ford (FF), Tennessee	291.3 (181.0)	8,600	2007	72	9.2	7.2	11.2
Frost Ford (FF), Tennessee	291.8 (181.3)	15,050	2004[b]	60	31.4	27	35.8
			2005[b]	60	24.2	20.1	28.3
			2006[b]	60	27.1	22.6	31.6
			2007[b]	60	45.9	38.5	53.3
			2008[b]	60	68.4	58.8	78
			2009[b]	91	42.9	37	48.8
			2010	80	55.9	47.7	65.5
			2011	80	53.5	47.4	60.4
			2012	80	50	44.4	56.2
			2013	80	44.3	38.6	50.7
			2014	80	43.8	38.4	49.8
Little E. Island, Tennessee	293.7 (182.5)	11,200	2005	60	19.3	16.2	22.4
Brooks Island, Tennessee	295.3 (183.5)	~6,000	1979[a]	26	11.4	NA	NA
			1988[a]	26	9.7	6	13.4
			1994[a]	26	13.7	NA	NA
			1999[a]	26	40.8	32	49.6
			2004[a]	26	21.3	16.9	25.7
			2005[b]	60	21.5	13.6	29.2
Webb Island, Tennessee	301.7 (187.5)	4,576	2006	60	22.8	18.4	27.2
Kyles Ford, Tennessee	305.1 (189.6)	~15,000	1979[a]	41	31	NA	NA
			1988[a]	41	14.3	9.6	19
			1994[a]	41	37.6	NA	NA
			1999[a]	41	95.9	81.5	110.3
			2004[a]	41	74.3	60.3	88.3
			2004[b]	146	43.8	35.8	51.8

Table 1, continued.

Site Location Name	River Kilometer (river mile)	Total Site Area (m^2)	Year(s) Sampled	No. (N) 0.25 m^2 Quadrats/yr	Mean Density/m^2	Lower 95% CI	Upper 95% CI
Wallen Bend (WB), Tennessee	309.5 (192.3)	16,933	2007	120	22	18.7	25.4
Wallen Bend (WB), Tennessee	309.6 (192.4)	3,182	2004[b]	60	13.7	10.9	16.5
			2005[b]	60	12.9	10.2	15.6
			2006[b]	60	15.1	12.2	18
			2007[b]	60	21.3	18	24.6
			2008[b]	60	30.2	23.8	36.6
			2009[b]	60	28.5	23.2	33.8
			2010	80	27.3	23.2	32.2
			2011	80	17.2	13.9	21.3
			2012	80	18.8	14.5	24.3
			2013	80	17.2	13.9	21.2
			2014	80	18.6	14.6	23.8
Speers Ferry, Virginia	339.7 (211.1)	~4,000	1979[a]	40	3.7	NA	NA
			1988[a]	40	2.7	1.7	3.7
			1994[a]	40	2.9	NA	NA
			1999[a]	40	4.8	2.4	7.2
			2004[a]	40	4.7	2.6	6.8
			2009[b]	80	5	3.6	6.4
Pendleton Island (PI), Virginia	364.2 (226.3)	55,503	1979[a]	40	24.6	NA	NA
			1987[c]	*22	18.7	15	22.4
			1994[a]	40	11.2	NA	NA
			1999[a]	40	12.4	10	14.8
			2004[a]	40	4.6	2.9	6.4
			2009[b]	360	0.66	0.5	0.9
			2014	187	1.1	0.8	1.5
Semones Island (SEI), Virginia	378.3 (235.1)	~10,000	1983[a]	40	7.7	NA	NA
			1988[a]	40	4.6	NA	NA
			1994[a]	40	6.5	NA	NA
			1999[a]	40	4.2	2.7	5.7
			2004[a]	40	1.7	0.7	2.7
			2009[b]	124	0.61	0.3	0.9
			2014	133	0.69	0.6	0.8

15%—to determine when density would return to baseline. Additionally, we estimated mussel losses over time and into the future based on departures in density and abundance from baseline conditions, i.e., minus each year's density from 1979 to 2014 and from 2015 to 2044 under the four growth rate scenarios. Scientific and common names of mussels follow Williams et al. (2017).

Survey methods.—Sampling methodology followed that of Jones et al. (2014) and was conducted in late summer or early fall when water levels were low and young-of-the-year and older juvenile mussels had reached sizes adequate for detection (e.g., >10 mm). Most mussel species in the Clinch River prefer shallow water (<1 m) containing gravel shoals, which served as sample sites for our survey. This habitat is abundant in the river but interspersed with longer, slower-flowing deeper pools (>1 RKM) containing poorer quality mussel habitat. Typical lengths of gravel shoals were about 100–200 m but were occasionally longer. We determined the upstream and downstream limits of sampling sites, which are very discrete in the river, by visually inspecting substrate composition (e.g., noting an abrupt change from suitable gravel substrate to unsuitable bedrock or soft sediments), water depth, flow velocity, and general presence or absence of mussels. The same upstream and downstream boundaries were used at sites sampled annually. We measured, and subtracted from analyses, any small, exposed gravel bars and islands without mussels but within the immediate shoal area. Using a standard 100-m tape, we measured site dimensions (length and width) and then determined the total area (m^2) of the sample sites by multiplying mean river width, measured at 10–20 m intervals, by total reach length (Table 1). At PI in summer 2016, we measured stream width and length at 10-m intervals along the length of each channel using a rangefinder (Wildgame Innovations R400 HALO 6 × 24, Wildgame Innovations

Table 2. Abundance of live mussels of each species sampled during quantitative quadrat surveys conducted at Swan Island (SI), Frost Ford (FF), Wallen Bend (WB), and other sites (see Table 1) from 2004 to 2014 in the Clinch River, Hancock County, Tennessee. Data from 2004 to 2009 are from Jones et al. (2014). Sample sizes per year are available in Table 1.

	2004–2009				2010–2014			
Scientific Name	SI	FF	WB	Other Sites	SI	FF	WB	All Sites and Years
(1) *Actinonaias ligamentina*	401	173	148	318	184	184	120	1,528
(2) *Actinonaias pectorosa*	759	189	217	533	781	260	235	2,974
(3) *Alasmidonta marginata*	1	0	0	0	2	1	1	5
(4) *Amblema plicata*	1	0	1	0	0	0	0	2
(5) *Cyclonaias pustulosa*	3	0	0	4	7	5	0	19
(6) *Cyclonaias tuberculata*	11	35	18	24	11	33	9	141
(7) *Cyprogenia stegaria*	12	13	1	10	15	20	0	71
(8) *Dromus dromas*	84	62	2	26	104	67	0	345
(9) *Epioblasma brevidens*	40	51	30	59	53	65	20	318
(10) *Epioblasma capsaeformis*	80	1,616	363	464	198	1,763	314	4,798
(11) *Epioblasma triquetra*	15	4	2	8	17	12	1	59
(12) *Eurynia dilatata*	2	68	68	77	1	170	89	475
(13) *Fusconaia cor*	0	1	5	1	0	3	19	29
(14) *Fusconaia cuneolus*	0	7	13	4	1	10	17	52
(15) *Fusconaia subrotunda*	8	19	5	32	8	31	8	111
(16) *Hemistena lata*	9	28	0	21	12	29	5	104
(17) *Lampsilis fasciola*	18	28	34	52	28	56	40	256
(18) *Lampsilis ovata*	11	6	3	8	5	10	3	46
(19) *Lasmigona costata*	3	1	1	5	7	6	2	25
(20) *Lemiox rimosus*	1	15	8	17	0	28	1	70
(21) *Ligumia recta*	1	0	1	1	2	1	0	6
(22) *Margaritifera monodonta*	0	0	0	1	1	0	0	2
(23) *Medionidus conradicus*	167	1,105	574	973	289	1,305	648	5,061
(24) *Plethobasus cyphyus*	2	16	1	8	5	34	1	67
(25) *Pleurobema cordatum*	1	0	0	0	0	0	0	1
(26) *Pleurobema oviforme*	0	1	1	0	0	1	0	3
(27) *Pleurobema plenum*	0	14	0	7	3	27	0	51
(28) *Pleurobema rubrum*	1	0	0	0	1	0	0	2
(29) *Pleuronaia barnesiana*	1	1	0	1	1	2	0	6
(30) *Pleuronaia dolabelloides*	0	0	0	1	0	0	0	1
(31) *Potamilus alatus*	0	0	0	1	0	0	0	1
(32) *Ptychobranchus fasciolaris*	114	71	43	117	120	107	69	641
(33) *Ptychobranchus subtentus*	267	313	263	519	297	406	297	2,362
(34) *Strophitus undulatus*	0	1	0	3	1	5	0	10
(35) *Theliderma cylindrica*	1	5	1	6	3	9	0	25
(36) *Truncilla truncata*	0	0	0	1	0	0	0	1
(37) *Villosa iris*	1	20	21	29	12	44	22	149
(38) *Villosa vanuxemensis*	0	0	0	1	0	0	0	1
Total	2,015	3,863	1,824	3,332	2,169	4,694	1,921	19,818
Total species	28	27	25	33	29	30	21	38

Inc., Broussard, LA); we used the data to calculate the square area of suitable habitat.

We collected quantitative data by systematic 0.25 m^2 quadrat samples placed on transect lines positioned perpendicular along the width of the river. Both transects and quadrats were evenly spaced throughout the delineated shoal area. Quarter-meter quadrats were delineated using a 0.5 m $\times$ 0.5 m frame constructed of 12 mm diameter rebar welded at the corners. Using a mask and snorkel, surveyors visually searched for mussels while excavating substrate approximately 15–20 cm in depth within each quadrat. Live mussels were collected from quadrat excavations, placed in a mesh bag, and brought to the river bank for identification and measurement. We identified the mussels to species, and using digital calipers,

Table 3. Total count (from Table 2), proportion, density, and abundance category of live mussels for species sampled during quantitative quadrat surveys conducted at Swan Island, Frost Ford, Wallen Bend, and other sites (see Table 1) from 2004 to 2014 in the Clinch River, Hancock County, Tennessee. Categories include Abundant (>1/m^2), Common (<1–0.1/m^2), Uncommon (<0.1–0.01/m^2), and Rare (<0.01/m^2).

Species	Total Count	Proportion (%)	Density/m^2	Category
(1) *Medionidus conradicus*	5,061	25.54	7.47	Abundant
(2) *Epioblasma capsaeformis*	4,798	24.21	7.08	Abundant
(3) *Actinonaias pectorosa*	2,974	15.00	4.39	Abundant
(4) *Ptychobranchus subtentus*	2,362	11.92	3.49	Abundant
(5) *Actinonaias ligamentina*	1,528	7.71	2.26	Abundant
(6) *Ptychobranchus fasciolaris*	641	3.23	0.95	Common
(7) *Eurynia dilatata*	475	2.40	0.70	Common
(8) *Dromus dromas*	345	1.74	0.51	Common
(9) *Epioblasma brevidens*	318	1.60	0.47	Common
(10) *Lampsilis fasciola*	256	1.29	0.38	Common
(11) *Villosa iris*	149	0.75	0.22	Common
(12) *Cyclonaias tuberculata*	141	0.71	0.21	Common
(13) *Fusconaia subrotunda*	111	0.56	0.16	Common
(14) *Hemistena lata*	104	0.52	0.15	Common
(15) *Cyprogenia stegaria*	71	0.36	0.10	Common
(16) *Lemiox rimosus*	70	0.35	0.10	Common
(17) *Plethobasus cyphyus*	67	0.34	0.10	Common
(18) *Epioblasma triquetra*	59	0.30	0.09	Uncommon
(19) *Fusconaia cuneolus*	52	0.26	0.08	Uncommon
(20) *Pleurobema plenum*	51	0.26	0.07	Uncommon
(21) *Lampsilis ovata*	46	0.23	0.07	Uncommon
(22) *Fusconaia cor*	29	0.15	0.04	Uncommon
(23) *Lasmigona costata*	25	0.13	0.04	Uncommon
(24) *Theliderma cylindrica*	25	0.13	0.04	Uncommon
(25) *Cyclonaias pustulosa*	19	0.10	0.03	Uncommon
(26) *Strophitus undulatus*	10	0.05	0.01	Uncommon
(27) *Pleuronaia barnesiana*	6	0.03	0.009	Rare
(28) *Ligumia recta*	6	0.03	0.009	Rare
(29) *Alasmidonta marginata*	5	0.03	0.007	Rare
(30) *Pleurobema oviforme*	3	0.02	0.004	Rare
(31) *Margaritifera monodonta*	2	0.01	0.003	Rare
(32) *Amblema plicata*	2	0.01	0.003	Rare
(33) *Pleurobema rubrum*	2	0.01	0.003	Rare
(34) *Pleuronaia dolabelloides*	1	<0.01	0.001	Rare
(35) *Pleurobema cordatum*	1	<0.01	0.001	Rare
(36) *Potamilus alatus*	1	<0.01	0.001	Rare
(37) *Truncilla truncata*	1	<0.01	0.001	Rare
(38) *Villosa vanuxemensis*	1	<0.01	0.001	Rare
Totals	19,818	100	29.25	
Total ¼ m^2 quadrats excavated	2,721			

we measured for total shell length anterior to posterior (nearest 0.1 mm) before returning them to their approximate position of collection. Population densities (N/m^2) were calculated from the means of the quadrat samples at each site. Specifically, we multiplied mean density from 0.25 m^2 quadrat samples by four to derive an estimate of mean density per m^2 and then multiplied that figure by the total square area of each site to derive an estimate of mussel abundance. At PI, quadrat samples were collected in 2009 and 2014 from the entire left-descending channel, starting from the downstream end of the channel and ending at the upstream beginning of the channel (see Fig. 2 and red dots marked in left-descending channel). Ahlstedt et al. (2016) and Dennis (1989) collected quadrat samples from the upper third of the left-descending channel from 1979 to 2004.

Data analysis.—We used a generalized linear model (GLM) to test for significance of trends in the mussel assemblage time series data collected from 1979 to 2004 at

Table 4. Proportional percentage of each species in the Pendleton Island mussel assemblage in the Clinch River, Scott County, Virginia, from 1979 to 2014. Data are from quadrat sampling conducted by the following: [A]Ahlstedt et al. (2016), [B]Dennis (1989), [C]Jones et al. (2014), and [D]current study. Sample sizes per year are available in Table 1.

Scientific Name	1979[A]	1987[B]	1994[A]	1999[A]	2004[A]	2009[C]	2014[D]
(1) *Actinonaias ligamentina*	13.82	19.5	23.21	20.16	10.87	25.69	32.07
(2) *Actinonaias pectorosa*	14.63	21.9	30.36	34.68	39.13	17.08	13.20
(3) *Alasmidonta marginata*	0	0	0	0	0	0	0
(4) *Amblema plicata*	3.25	1.9	0.89	2.42	8.70	6.77	9.43
(5) *Cyclonaias pustulosa*	0	0	0	0	0	0	0
(6) *Cyclonaias tuberculata*	4.47	3.3	4.46	5.65	13.04	6.77	1.89
(7) *Cyprogenia stegaria*	0	0	0	0	0	0	0
(8) *Dromus dromas*	0	0	0	0	0	0	0
(9) *Elliptio crassidens*	0	0	0	0	0	0	0
(10) *Epioblasma brevidens*	0	0	0	0	0	1.69	1.89
(11) *Epioblasma capsaeformis*	3.25	0	0	0	0	0	0
(12) *Epioblasma gubernaculum*	0	0	0	0	0	0	0
(13) *Epioblasma triquetra*	0	0.5	0	0	0	0	0
(14) *Eurynia dilatata*	25.61	13.5	12.5	6.45	4.35	1.69	1.89
(15) *Fusconaia cor*	1.22	0	3.57	0	4.35	1.69	0
(16) *Fusconaia cuneolus*	4.47	11.6	2.68	5.65	0	0	0
(17) *Fusconaia subrotunda*	6.91	5.1	17.86	15.32	2.17	0	0
(18) *Hemistena lata*	0	0	0	0	0	0	0
(19) *Lampsilis abrupta*	0	0	0	0	0	0	0
(20) *Lampsilis fasciola*	0.81	1.4	0.89	2.42	0	1.69	3.77
(21) *Lampsilis ovata*	2.03	0.9	0	0	2.17	0	0
(22) *Lasmigona costata*	5.28	4.2	0.89	1.61	0	0	0
(23) *Lemiox rimosus*	0	0.5	0	0	0	1.69	0
(24) *Leptodea fragilis*	0.41	0	0	0	0	0	0
(25) *Ligumia recta*	0.41	0.5	0	0	0	0	0
(26) *Margaritifera monodonta*	0	0	0	0	0	0	0
(27) *Medionidus conradicus*	0.81	0	0	0.81	0	1.69	5.66
(28) *Plethobasus cyphyus*	0	0.5	0	0	0	0	0
(29) *Pleurobema cordatum*	0	0.5	0	0	0	0	0
(30) *Pleurobema oviforme*	0	0	0	0	0	0	0
(31) *Pleurobema rubrum*	0	0	0.89	0	0	0	0
(32) *Pleuronaia barnesiana*	0.41	6.5	0	0	0	0	0
(33) *Pleuronaia dolabelloides*	0	0	0	0	0	0	0
(34) *Potamilus alatus*	0.41	0	0	0	0	1.69	0
(35) *Ptychobranchus fasciolaris*	1.63	0.9	0.89	2.42	6.52	16.92	5.66
(36) *Ptychobranchus subtentus*	4.47	0.5	0.89	0.81	0	0	0
(37) *Strophitus undulatus*	0	0	0	0	0	0	0
(38) *Theliderma cylindrica*	5.28	0.9	0	0	0	1.69	0
(39) *Theliderma intermedia*	0	0	0	0	0	0	0
(40) *Theliderma sparsa*	0	0	0	0	0	0	0
(41) *Truncilla truncata*	0	0	0	0	0	0	0
(42) *Venustaconcha trabalis*	0.41	0.5	0	0	0	0	0
(43) *Villosa fabalis*	0	0	0	0	0	0	0
(44) *Villosa iris*	0	0.9	0	1.61	8.70	12.0	24.52
(45) *Villosa vanuxemensis*	0	0	0	0	0	1.69	0
Total individuals	246	206	112	124	46	59	53
Total species	21	21	13	13	10	15	10

Table 5. Relative proportion of each mussel species in the Clinch River at Pendleton Island (PI), Scott County, Virginia, and at sites in Hancock County, Tennessee, where A = data are from Table 3 and represent mean proportion of species at sites in Tennessee from 2004 to 2014; B = data are from Table 4 and represents proportion of each species in 1979 at PI; C = mean of data in columns A and B and represents proposed baseline proportion of each species for PI mussel assemblage; D = proposed baseline abundance of each species at PI based on a mussel assemblage density of $25/m^2$.

Species	A	B	C	D
(1) *Actinonaias ligamentina*	7.71	13.82	10.755	149,234
(2) *Actinonaias pectorosa*	15.0	14.63	14.815	205,569
(3) *Alasmidonta marginata*	0.03	0	0.015	208
(4) *Amblema plicata*	0.01	3.25	1.63	22,617
(5) *Cyclonaias pustulosa*	0.01	0	0.005	69
(6) *Cyclonaias tuberculata*	0.71	4.47	2.58	35,799
(7) *Cyprogenia stegaria*	0.36	0	0.18	2,498
(8) *Dromus dromas*	1.74	0	0.87	12,072
(9) *Elliptio crassidens*	0	0	0	0
(10) *Epioblasma brevidens*	1.6	0	0.8	11,101
(11) *Epioblasma capsaeformis*	24.21	3.25	13.73	190,514
(12) *Epioblasma gubernaculum*	0	0	0	0
(13) *Epioblasma triquetra*	0.3	0	0.15	2,081
(14) *Eurynia dilatata*	2.4	25.61	14.005	194,330
(15) *Fusconaia cor*	0.15	1.22	0.685	9,505
(16) *Fusconaia cuneolus*	0.26	4.47	2.365	32,816
(17) *Fusconaia subrotunda*	0.56	6.91	3.725	51,687
(18) *Hemistena lata*	0.52	0	0.26	3,608
(19) *Lampsilis abrupta*	0	0	0	0
(20) *Lampsilis fasciola*	1.29	0.81	1.05	14,570
(21) *Lampsilis ovata*	0.23	2.03	1.13	15,680
(22) *Lasmigona costata*	0.13	5.28	2.705	37,534
(23) *Lemiox rimosus*	0.35	0	0.175	2,428
(24) *Leptodea fragilis*	0	0.41	0.205	2,845
(25) *Ligumia recta*	0.03	0.41	0.22	3,053
(26) *Margaritifera monodonta*	0.01	0	0.005	69
(27) *Medionidus conradicus*	25.54	0.81	13.165	182,674
(28) *Plethobasus cyphyus*	0.34	0	0.17	2,359
(29) *Pleurobema cordatum*	0.01	0	0.005	69
(30) *Pleurobema oviforme*	0.02	0	0.01	139
(31) *Pleurobema rubrum*	0.01	0	0.005	69
(32) *Fusconaia barnesiana*	0.03	0.41	0.22	3,053
(33) *Pleuronaia dolabelloides*	0.01	0	0.005	69
(34) *Potamilus alatus*	0.01	0.41	0.21	2,914
(35) *Ptychobranchus fasciolaris*	3.23	1.63	2.43	33,718
(36) *Ptychobranchus subtentus*	11.92	4.47	8.185	113,573
(37) *Strophitus undulatus*	0.5	0	0.25	3,469
(38) *Theliderma cylindrica*	0.13	5.28	2.705	37,534
(39) *Theliderma intermedia*	0	0	0	0
(40) *Theliderma sparsa*	0	0	0	0
(41) *Truncilla truncata*	0.01	0	0.005	69
(42) *Venustaconcha trabalis*	0	0.41	0.205	2,844
(43) *Villosa fabalis*	0	0	0	0
(44) *Villosa iris*	0.75	0	0.365	5,065
(45) *Villosa vanuxemensis*	0.01	0	0.005	69
Total				1,387,574

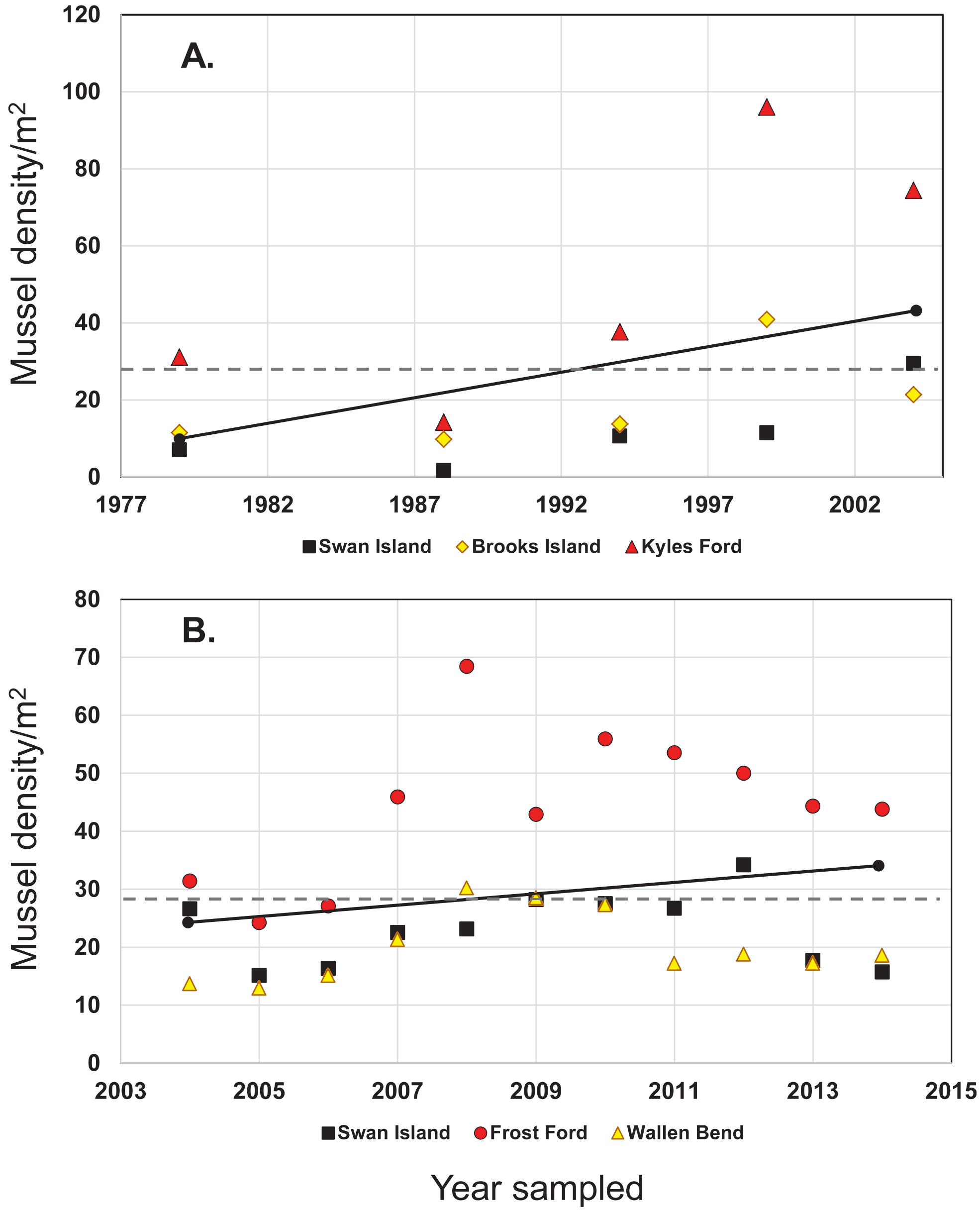

Figure 3. Panel A: Time series of mean mussel density from 1979 to 2004 at three sites, Swan Island, Brooks Island, and Kyles Ford, in the Clinch River, Hancock County, Tennessee; data are from Ahlstedt et al. (2016). Solid line is linear regression [$y = 1.3982x + (-2{,}758.9174)$] of increasing density over all sites ($P < 0.001$) and years, and broken horizontal line is mean (27.32/m^2) over all sites and years. Panel B: Time series of mean mussel density sample annually from 2004 to 2014 at three sites, Swan Island, Frost Ford, and Wallen Bend, in the Clinch River, Hancock County, Tennessee; data are from Jones et al. (2014) and from the current study. Solid line is linear regression [$y = 0.8861x + (-1{,}751.0382)$] of increasing density over all sites ($P = 0.003$) and years, and broken horizontal line is mean (29.1/m^2) over all sites and years. Density data from all sites are available in Table 1.

SI, Brooks Island, and Kyles Ford and from 2004 to 2014 at SI, FF, and WB, and from 1979 to 2014 at PI by utilizing data from Ahlstedt et al. (2016), Jones et al. (2014), and the current study. A GLM also was used to test for significance of trends in density for six mussel species at SI, FF, and WB from 2004 to 2014. We tested data for normality using the Shapiro-Wilk test; data were not normally distributed and modeled in the GLM using a Poisson distribution and the log-link function. We used simple linear regression to produce trend lines for assemblage density data. To test for differences in mussel assemblage density at PI between the 2009 and 2014 sample years, we used a two-sample *t*-test assuming unequal variances. All statistical tests were implemented using the program R (R Core Development Team 2006).

RESULTS

Baseline conditions, Clinch River, Tennessee.—Mussel density significantly increased ($P < 0.001$) at monitoring sites

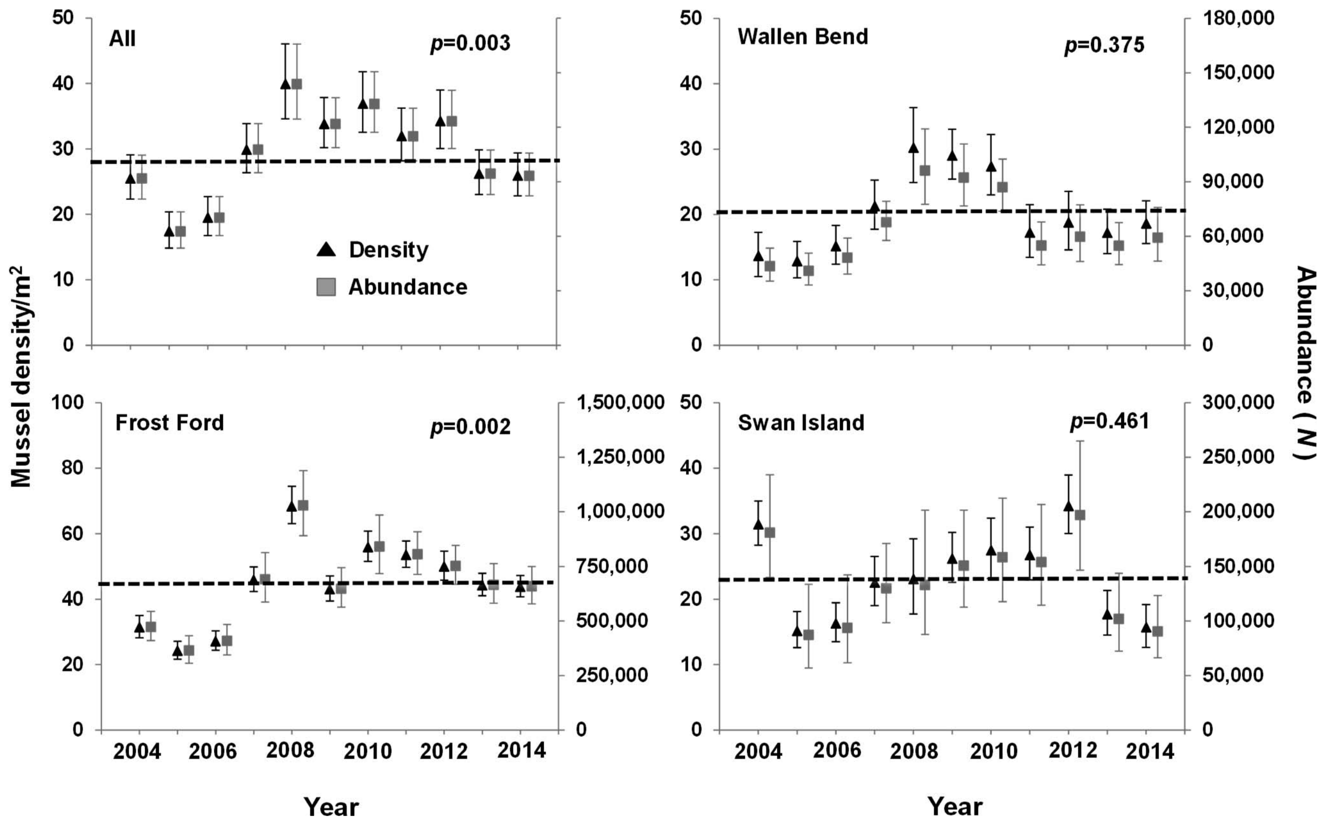

Figure 4. Time series of mean mussel density from 2004 to 2014 at Swan Island, Frost Ford, and Wallen Bend in the Clinch River, Hancock County, Tennessee. Error bars represent 95% confidence intervals, where nonoverlapping intervals among sample years indicate significant ($P < 0.05$) differences. Broken line is the mean of all years. Data from 2004 to 2009 are from Jones et al. (2014).

in the Tennessee section of the Clinch River over a 25-yr period from a mean of 16.5/m^2 in 1979 to a mean of 41.7/m^2 in 2004; mean density at sampled sites over this period was 27.1/m^2 (Table 1 and Fig. 3). Using the regression equation in Figure 3 [$y = 1.3982x + (-2{,}758.9174)$], predicted density in 1979 was 8.1/m^2, and in 2004 it was 43.1/m^2. The corresponding mussel assemblage growth rate over this period was 81%, an increase of 2.26% per year. Site density was lowest at SI in 1988 at 1.6/m^2 and highest at Kyles Ford in 1999 at 95.9/m^2 (Table 1). Of the three sites (SI, FF, WB) sampled annually from 2004 to 2014, mussel density significantly increased ($P = 0.003$) at monitoring sites over this 10-yr period in the Tennessee section of the Clinch River from a mean of 23.9/m^2 in 2004 to a mean of 26.0/m^2 in 2014; mean density at sampled sites over this period was 29.1/m^2 (Table 1 and Fig. 3). Using the regression equation in Figure 3 [$y = 0.8861x + (-1{,}751.0382)$], predicted density in 2004 was 24.7/m^2, and in 2014 it was 33.6/m^2. The corresponding mussel assemblage growth rate over this period was 27%, an increase of 1.3% per year. Mean density and abundance were highest at FF at 44.3/m^2 and 666,715 mussels, where density increased significantly ($P = 0.002$) over the study period, followed by SI at 22.8/m^2 and 131,328 mussels and WB at 20.1/m^2 and 63,958 mussels, where density remained stable and did not significantly increase or decrease (Fig. 4). Densities and abundances fluctuated at these three sites, reaching their highest levels at FF and WB in 2008 and SI in 2012 and their lowest levels at all three sites in 2005. By 2014, mussel density at all three sites had returned to at or below each site's mean density.

Including samples from 2004 to 2009 (Jones et al. 2014), a total of 38 mussel species were collected live in quadrat samples at the 12 sites in the Tennessee section of the Clinch River from 2004 to 2014 (Table 2). All species sampled over this 10-yr period also were sampled from 2004 to 2009; therefore, no additional species were sampled from 2010 to 2014, with the following six species not collected during this latter period: *Amblema plicata*, *Pleurobema cordatum*, *Pleuronaia dolabelloides*, *Potamilus alatus*, *Truncilla truncata*, and *Villosa vanuxemensis*. We sampled a total of 30 species at SI, with 28 species sampled from 2004 to 2009 and 29 species sampled from 2010 to 2014. A total of 30 species were sampled at FF, with 27 species sampled from 2004 to 2009 and 29 species sampled from 2010 to 2014. A total of 28 species were sampled at WB, with 25 species sampled from 2004 to 2009, and 21 species sampled from 2010 to 2014. We sampled a total of 33 species at other sites from 2004 to 2009, with the aforementioned six species sampled only at these sites and not at SI, FF, and WB.

Five lampsiline species were abundant, each typically

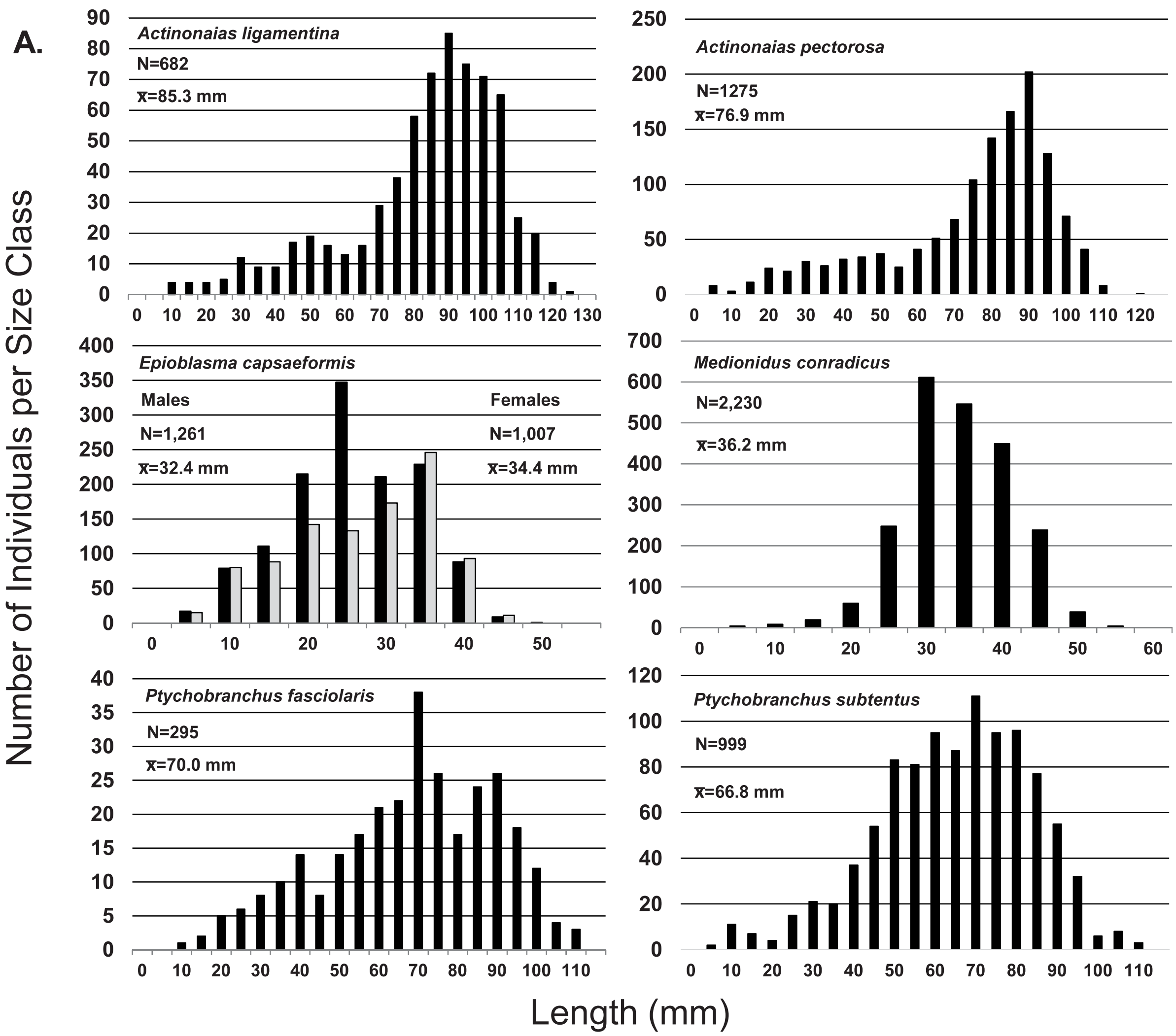

Figure 5. Panel A: Length frequency histograms of the six most abundant species sampled from 2010 to 2014 in the Clinch River, Hancock County, Tennessee. Panel B: Length frequency histograms of the six most abundant species sampled in 2009 and 2014 at Pendleton Island in the Clinch River, Scott County, Virginia.

occurring at a density $>1/m^2$ and together making up >80% of the assemblage: *Medionidus conradicus* (25.5%), *Epioblasma capsaeformis* (24.2%), *Actinonaias pectorosa* (15.0%), *Ptychobranchus subtentus* (11.9%), and *A. ligamentina* (7.7%). In addition, *Ptychobranchus fasciolaris* (3.2%) was common (Table 3). These six species' size-class frequency distributions indicate they have been recruiting annually from 2004 to 2014, with smaller, younger mussels well represented in samples (Fig. 5). Individuals of the relatively short-lived *M. conradicus* and *E. capsaeformis* <20–30 mm were typically ~3–4 yr old (Scott 1994; Jones and Neves 2011), while individuals <50–70 mm of the latter four longer-lived species were typically ~4–5 yr old (Scott 1994; Henley et al. 2001). Densities of these six species varied among sites and years at the three sites sampled annually (Fig. 6). Density of *A. ligamentina* at SI ranged from a low of $2.6/m^2$ in 2014 to high of $7.1/m^2$ in 2004; at FF, it ranged from $1.4/m^2$ in 2005 to $2.5/m^2$ in 2010; at WB, it ranged from $0.9/m^2$ in 2012 to $2.3/m^2$ in 2006. Density of *A. pectorosa* at SI ranged from a low of $5.1/m^2$ in 2006 to a high of $11.5/m^2$ in 2012; at FF, it ranged from $1.2/m^2$ in 2005 to $3.0/m^2$ in 2014; at WB, it ranged from $1.0/m^2$ in 2004 to $2.9/m^2$ in both 2007 and 2009. In contrast, density of *E. capsaeformis* fluctuated greatly at all three sites. At SI, its initial density was $0.7/m^2$ in 2004; it reached a low of $0.1/m^2$ in 2006, increased to $3.5/m^2$ in 2012, and then decreased to $1.3/m^2$ by 2014. Similarly, at FF, the initial density of *E. capsaeformis* was $7.5/m^2$ in 2004; it reached a low of $5.4/m^2$ in 2005, increased to $40.0/m^2$ in 2008, and then decreased to $13.9/m^2$ by 2014. The same pattern prevailed at WB, where initial density was $1.9/m^2$ in 2004; it decreased to $1.3/m^2$ in 2006, increased to $8.9/m^2$ in 2008, and then decreased to $3.0/m^2$ by 2014. The density of *M. conradicus* also fluctuated greatly at each site. At SI, its initial density was $1.9/m^2$ in 2004; it reached a low of $0.5/m^2$ in 2005, increased to $4.6/m^2$ in 2012, then decreased to $1.6/m^2$ by 2014. At FF, its density reached a low of $9.3/m^2$ in 2006 and a high of $16.6/m^2$ in 2010, and at WB, it reached a low of $3.8/m^2$ in 2004 and a high of $11.5/m^2$ in 2010. By comparison,

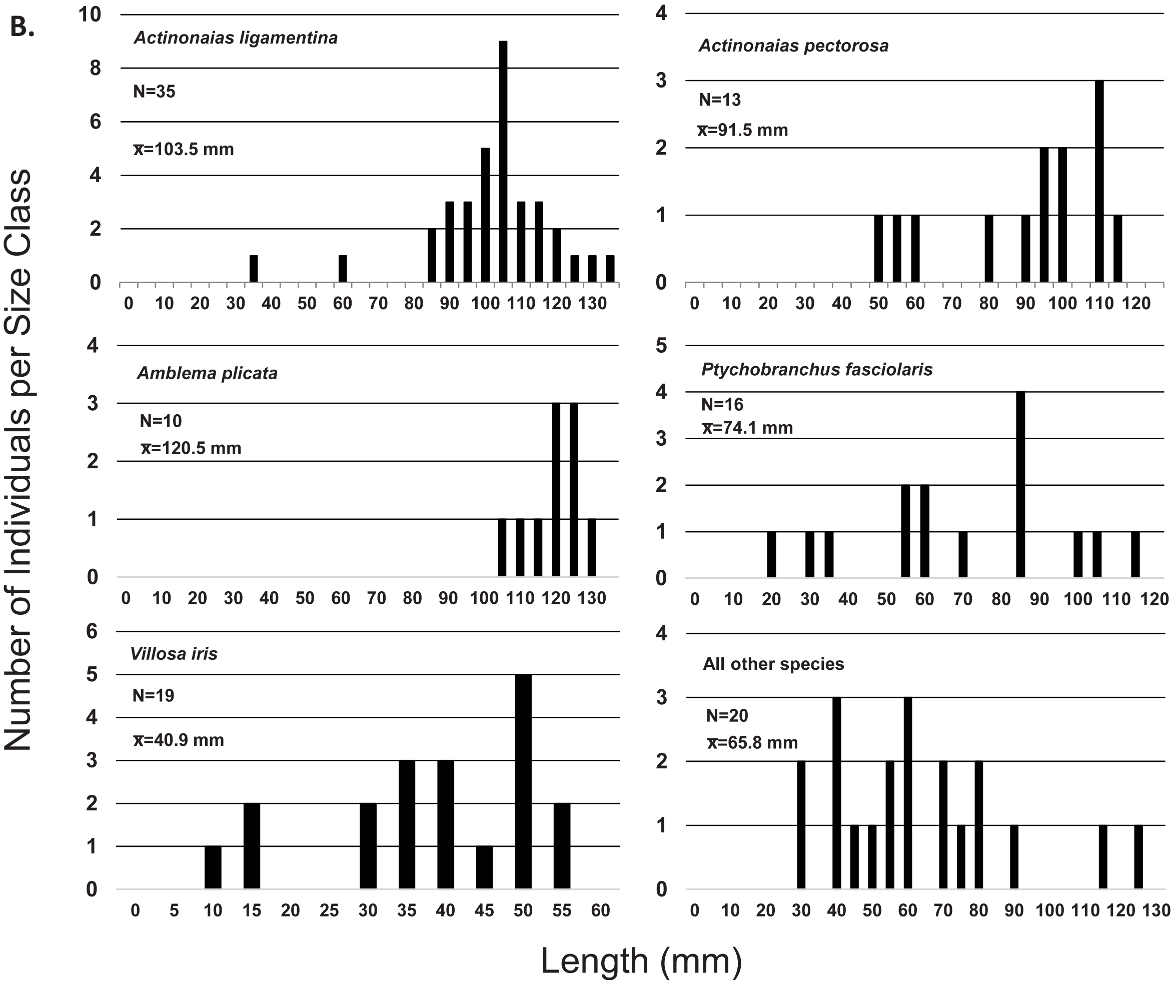

Figure 5, continued.

densities of *P. fasciolaris* were lower and more similar among sites and years, ranging at SI from 0.9/m^2 in 2005 to 1.7/m^2 in 2006, at FF from 0.4/m^2 in 2004 to 1.7/m^2 in 2013, and at WB from 0.3/m^2 in 2005 to 0.9/m^2 in 2012. Densities of *P. subtentus* also were similar among sites and years, ranging at SI from 1.6/m^2 in 2006 to 5.6/m^2 in 2004, at FF from 2.4/m^2 in 2007 to 4.9/m^2 in 2010, and at WB from 1.4/m^2 in 2005 to 4.7/m^2 in 2010. Despite the annual fluctuations at these three sites, densities of all six species remained stable and did not statistically increase or decrease from 2004 to 2014 (Fig. 6). All other species were common, uncommon, or rare in Tennessee, typically occurring at densities $<$1/m^2 per site, and collectively making up $<$10% of total abundance (Table 3). Specifically, 21 species were uncommon or rare, occurring at densities $<$0.10/m^2 and represented more than half of assemblage richness.

Baseline conditions, Pendleton Island, Virginia.—Of the 45 mussel species known from the Clinch River at Pendleton Island (PI), 29 have been collected live in quadrat samples from 1979 to 2014 (Table 4). The remaining 16 species, with the exception of *Villosa fabalis* (shell only), have been collected live from 1979 to 2014 but not in quadrat samples. Many of these species (e.g., *Epioblasma torulosa gubernaculum*, *Lampsilis abrupta*, *Quadrula intermedia*, and *Quadrula sparsa*) were represented by the collection of a single live individual in 1982 and 1983 during numerous visits to the site to assess species richness (R. J. Neves, USGS retired, personal communication). However, at least 29 species have been collected live or as fresh-dead shells during qualitative surveys since 1994 and thus are likely still extant at the site (see the Appendix). The greatest number of species sampled quantitatively was 21, which occurred in 1979 and 1987 when quadrat sample sizes were lower (40 and 22, respectively). In contrast, during the most recent sampling efforts (conducted in 2009 and 2014), a total of 15 and 10 species were observed, respectively, when quadrat sample sizes were much higher (360 and 187, respectively). Five species made up most of the relative abundance at PI in 2009 and 2014: *A. ligamentina* (2009 = 25.7%, 2014 = 32.1%), *Villosa iris* (2009 = 12.0%, 2014 = 24.5%), *A. pectorosa* (2009 = 17.1%, 2014 = 13.2%), *P. fasciolaris* (2009 = 16.9%, 2014 = 5.7%), and *A. plicata* (2009 = 6.8%, 2014 = 9.4%) (Table 4). Based on observed

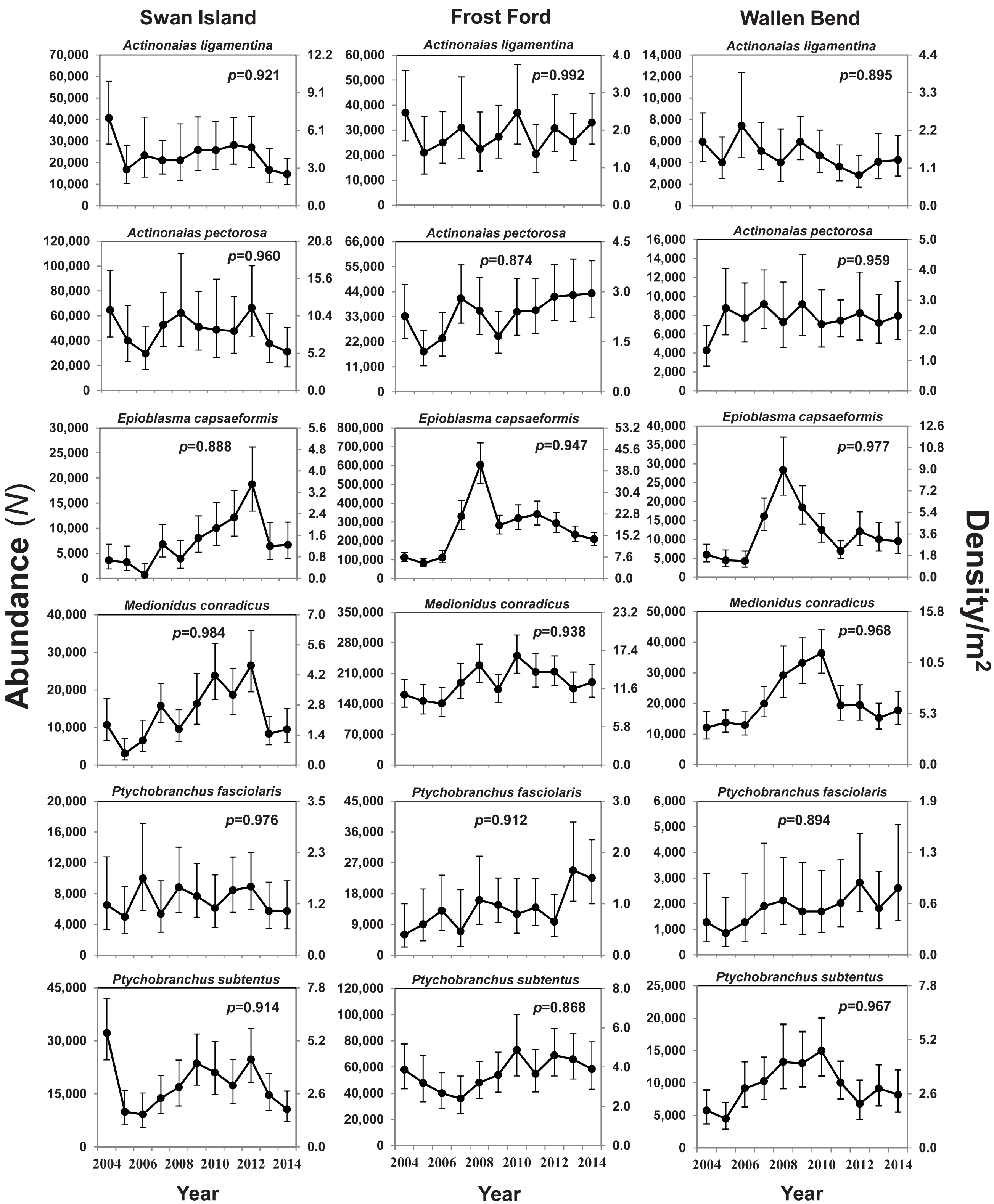

Figure 6. Time series of mean mussel density of the six most abundant species sampled annually from 2004 to 2014 at Swan Island, Frost Ford, and Wallen Bend in the Clinch River, Hancock County, Tennessee. None of the time series were significant over the study period. However, error bars represent 95% confidence intervals, where nonoverlapping intervals among sites or sample years indicate significant ($P < 0.05$) differences. Data from 2004 to 2008 for *Epioblasma capsaeformis* are from Jones and Neves (2011), and data from 2004 to 2009 for the other five species are from Jones et al. (2014).

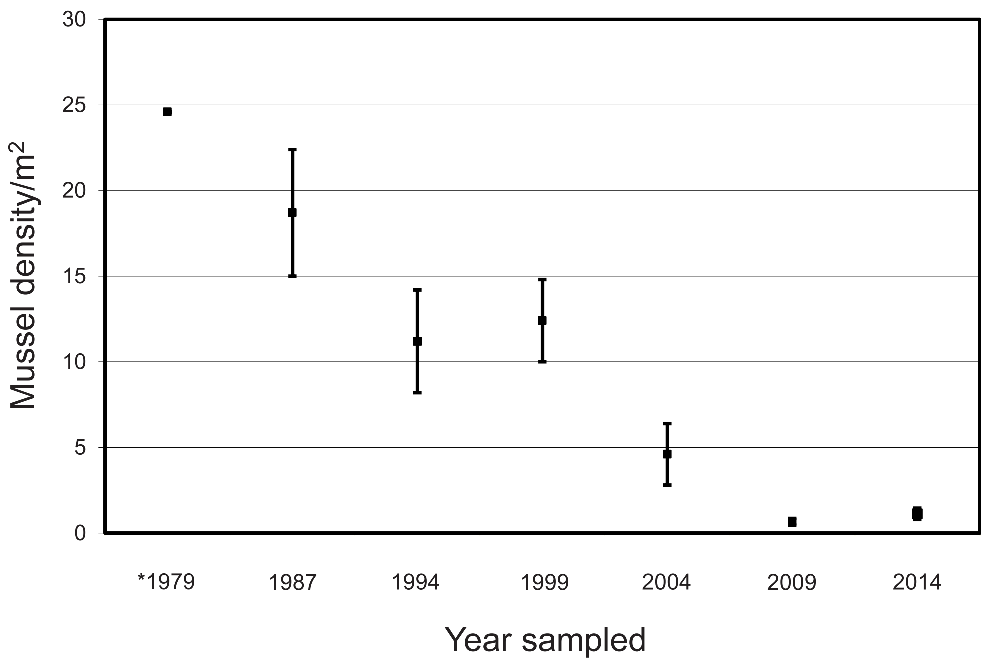

Figure 7. Time series of mean mussel density from 1979 to 2014 at Pendleton Island, Clinch River, Virginia, showing a severe and statistically significant decline in density ($P < 0.001$); data from 1979 to 2004 were collected by Ahlstedt et al. (2016) using a random survey design. Error bars represent 95% confidence intervals, where nonoverlapping intervals among sites or sample years indicate significant ($P < 0.05$) differences. Error bars are present for 2009 and 2014. *Raw data from 1979 were unavailable, but SE and 95% confidence intervals were likely similar to other sample years at the site with similar mean densities, e.g., the sample taken in 1987.

size-class frequency distributions and the presence of individuals <30–50 mm long, four of these species show evidence of recent recruitment (Fig. 5B). No small individuals of *A. plicata* were observed in either sampling year, but small and young individuals (<5 yr) of other species (e.g., *Lampsilis fasciola* and *M. conradicus*) were observed.

Our data, combined with that of Jones et al. (2014) and Ahlstedt et al. (2016) (see Fig. 7), demonstrate the following pattern in density and abundance of the mussel assemblage at PI: (1) in the late 1970s, density was ~25/m^2 with an abundance of nearly 1.4 million individuals, (2) from 1979 to 2009, density and abundance significantly declined ($P < 0.001$) to 0.7/m^2 and an abundance of ~37,000 individuals, and (3) from 2009 to 2014, density remained low but increased to 1.1/m^2 with an abundance of 50,000–60,000 individuals, significantly higher ($P = 0.005$) than the 2009 sample (Table 1 and Fig. 8). Mussel density upstream at Semones Island was ~8/m^2 in the early 1980s and then declined to 0.6/m^2 in 2009 (Jones et al. 2014) and 0.7/m^2 in 2014 (Table 1).

Projecting density and abundance forward 30 yr (2014–44), the mussel assemblage of PI returns to a baseline of 25/m^2 only if we assume a high growth rate of 15% per yr. If we assume a growth rate of 10% per year, density reaches 17.4/m^2 and an abundance of ~968,000 individuals in 2044. Under lower and arguably more realistic growth rate scenarios of 1% and 5%, density reaches just 1.4/m^2 (~75,000 individuals) and 4.3/m^2 (~240,000 individuals), respectively, by 2044.

Finally, we based mussel losses over time on departures in density and abundance from the baseline of 25/m^2 and an abundance of 1,387,575 mussels (Fig. 8). Losses can be viewed as follows: (1) the absolute loss (difference) in density or abundance from baseline in a specific year, (2) the total cumulative loss in density or abundance over a specified time period, (3) loss of ecosystem services provided by mussels in a specific year, and (4) the cumulative loss of services provided by mussels over a specified period. In 2014, for example, the absolute loss in mussel density was 24/m^2 with a loss in abundance of 1,332,072 mussels. In 2014, the ecosystem services provided by an equivalent of 1,332,072 mussels were lost; however, from 1979 to 2014, the cumulative ecosystem services provided by an equivalent of 27,514,980 mussels were lost. When these losses are projected forward in time, cumulatively, they can be staggering. For example, under the 1% growth rate scenario, from 1979 to 2044, the ecosystem services provided by an equivalent of 67.2 million mussel years would be lost (Fig. 8, panel B).

DISCUSSION

Patterns of Mussel Abundance and Species Richness in Tennessee

As demonstrated by Jones et al. (2014), Ahlstedt et al. (2016), and again in our study, it is evident that two broad and ongoing patterns of mussel abundance occur in the Clinch River, one of relative stability and high abundance in

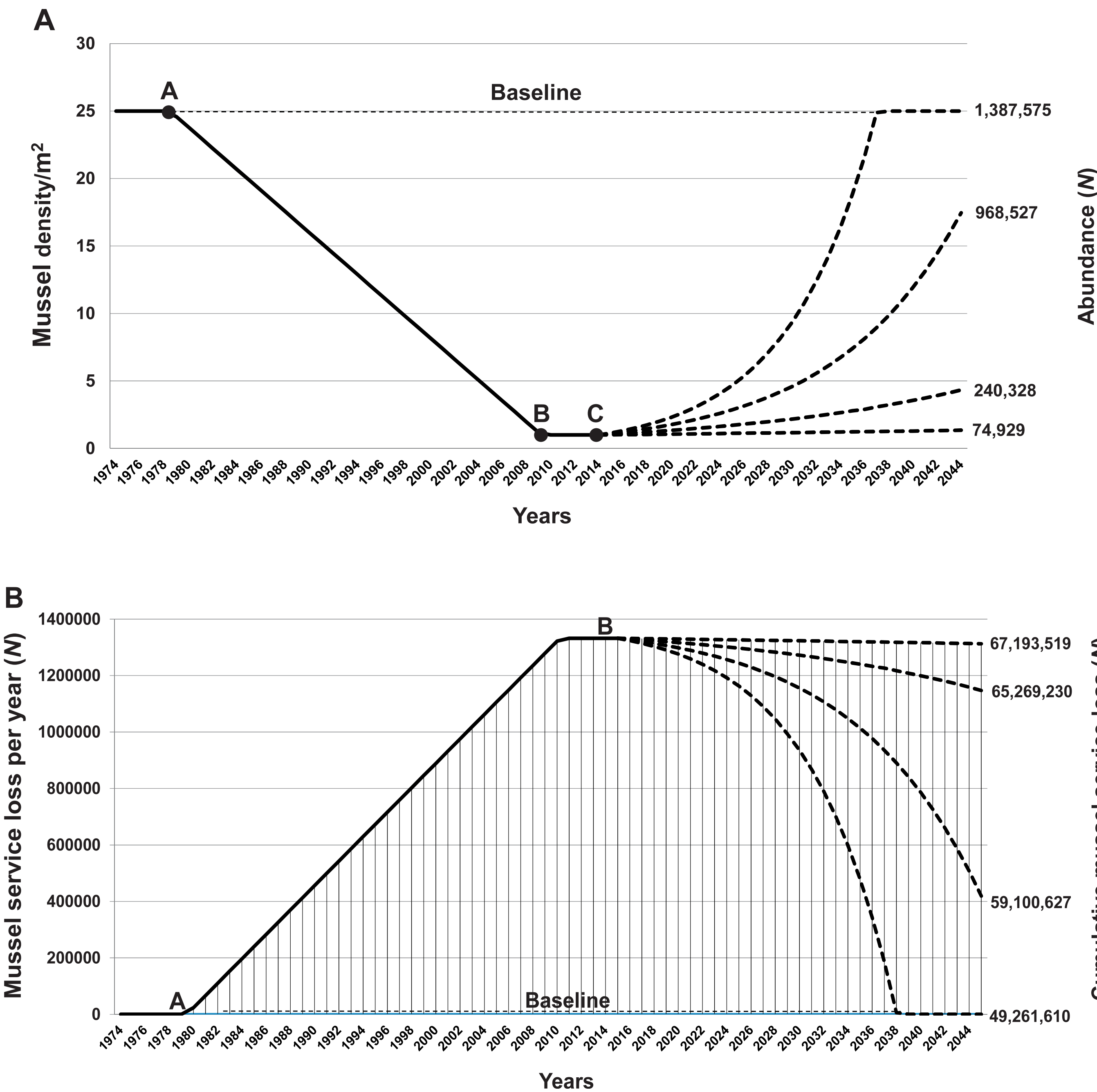

Figure 8. Panel A: Historical baseline mussel density of 25/m^2 at Pendleton Island, Scott County, Virginia, is represented by horizontal broken line beginning in 1979 and projected into the future until 2044. Point A represents the measured density of 25/m^2 sampled by in 1979 by Ahlstedt et al. (2016), and Point B represents the measured density of $\sim$1/m^2 sampled in 2009 by Jones et al. (2014). Declining solid straight line between points A and B is a linear regression ($y = 1{,}568 - 0.7797{*}X$) of the mean mussel density values from 1979 to 2009 shown in Figure 7. The horizontal straight line between points B and C represents a mean mussel density of $\sim$1/m^2 from 2009 to 2014. The broken curved lines represent the mussel assemblage increasing over time from 2014 until 2044 at a rate of 1%, 5%, 10%, and 15%, respectively. Panel B: Inverse mussel density curves of the mussel assemblage at Pendleton Island are shown to illustrate per year and cumulative mussel service losses from 1979 to 2044, using the above growth rates, where point A is 1979 and point B is 2014.

Tennessee, and one of severe decline and low abundance at PI and other sites in a 68-km section of the river from St. Paul, Virginia, downstream to approximately Clinchport, Virginia (RKM 411.5 to 343.3). In Tennessee, mussel abundance has steadily increased since the late 1970s, and beginning around 2004, it stabilized at the current density of nearly 30/m^2. In this section of river, mussel abundance varies among sites, years, and species, but we consider these fluctuations largely natural, driven by environmental factors such as stream discharge and fluctuations in host fish abundance, and generally not by anthropogenic stressors (Jones and Neves 2011).

Of the 38 mussel species sampled quantitatively in the Tennessee section of the river, six species made up the majority of mussel abundance from 2004 to 2014, and they exhibited marked differences in their population dynamics over time. For example, populations of *E. capsaeformis* and *M. conradicus* have been more variable, characterized by obvious periods of increase and decrease, and have driven much of the variability in assemblage density over time. The increase in abundance of *E. capsaeformis* was due to high recruitment of juveniles in 2008 and 2009, likely in response to favorable survival and growing conditions for both the species and its host fishes during the low stream discharges that occurred in the summers of 2007 and 2008 (Jones and Neves 2011). In contrast, populations of *A. ligamentina*, *A. pectorosa*, *P. fasciolaris*, and *P. subtentus* also made up a large percentage of the assemblage density in Tennessee, but their numbers were less variable; their populations were best characterized as stable over the study period. For all six species, recruitment occurred regularly, with juvenile mussels a dominant and easily measurable part of their population age class structure.

The remaining 32 species were much less abundant, and their population trends were difficult to discern because sampling variability masked population changes. Even under seemingly excellent water quality and habitat conditions in the Tennessee section of the river, these species occurred at densities $<1/m^2$. Thirteen of these species are listed as endangered; the Clinch River populations represent some of the best or only remaining populations of each respective species rangewide, and they are critical to the species' long-term survival. However, many of these species are locally uncommon or rare and have much larger populations in other sections of the river upstream in Virginia, in tributaries to the river, and in streams outside of the Clinch River drainage. For many of these species, the presence of a few small individuals in quadrat samples provides evidence of recruitment; hence, we expect them to persist as relatively small populations over the coming decades.

Setting Baseline Conditions at Pendleton Island, Virginia

The mussel assemblage at PI now occurs at a density far below its historically documented baseline of nearly $25/m^2$. Based on our interpretation of existing data, we believe that assemblage density prior to 1979 was likely higher. PI is the largest site in the river upstream of Norris Reservoir and historically contained the highest species richness. Thus, prior to habitat degradation, and assuming normal habitat conditions such as the current conditions in Tennessee, these two factors—large habitat size and historical species richness—suggest that PI is capable of supporting a mussel assemblage at even higher densities. Sites in Tennessee certainly have supported much higher mussel densities, for example, $95.9/m^2$ at Kyles Ford in 1999 and $68.4/m^2$ at FF in 2008 (Table 1). It is possible that the assemblage at PI was in decline prior to 1979. Shorter-lived species such as *E. capsaeformis* and *Leptodea fragilis* were rare then, and by 1983, the assemblage comprised mostly larger and older mussels, suggesting that recruitment of juveniles was failing (R. J. Neves, U.S. Geological Survey, retired, personal communication). Thus, a density of $25/m^2$ should be considered the minimum baseline for the mussel assemblage at PI.

Based on quadrat sampling from 1979 to 2014, species composition at PI has shifted in two ways. First, fewer species are present in the samples. In 2009 and 2014, species once common at the site were absent from sampling, as were many of the rare and endangered species that were regularly detected there. Notable examples include *Fusconaia cuneolus*, *Fusconaia subrotunda*, *Lasmigona costata*, and *P. subtentus*, all of which were common in the late 1970s and early 1980s. Other species, such as *Ligumia recta*, *Plethobasus cyphyus*, *Pleurobema rubrum*, and *Venustaconcha trabalis*, which were always rare at the site, are now extremely rare or are extirpated. Many of the extremely rare species that were never detected in quadrat samples but were detected by qualitative sampling techniques used at the site over the years, are likely extirpated, including *Hemistena lata*, *L. abrupta*, *T. truncata*, *Theliderma intermedia*, and *Theliderma sparsa*, none of which have been seen live in decades. Second, the mussel assemblage today is dominated by species that are either long-lived and/or tolerant to disturbances in the Upper Tennessee River system, namely, *A. ligamentina*, *A. pectorosa*, *A. plicata*, *L. fasciola*, *P. fasciolaris*, and *V. iris*. Proportional species compositions and abundances for PI, shown in Table 5, can be used as targets to evaluate recovery and restoration of the site in the future.

Recovery and Valuation of Mussels at Pendleton Island, Virginia

Assuming environmental conditions improve at PI, it will take decades for the mussel fauna to naturally recover. Because of the extirpation or extinction of some species at the site and throughout the river, and assuming populations comprising the assemblage grow at a low annual rate (1–2%), recovery to baseline density and species richness most likely is not possible over the next 30 yr without human intervention. The relatively intact mussel assemblage in the Tennessee section of the river, for example, grew at only ~2% per year from 1979 to 2014 (Fig. 3). It seems prudent and justified to assume low but arguably realistic population growth rates into the future at PI. Clearly, the magnitude of lost mussel resources and services at PI is extremely large, and our analysis does not include assessment of other sites (e.g., Semones Island) in the ~68-km affected reach, which would easily double estimated losses. Both valuation and a better understanding of the ecological consequences of these lost mussel resources and services are required so that natural resource managers can better understand the cost, recovery, and restoration needs of the fauna.

As a natural resource, mussels can be valued in a variety of ways, including for the market price of their shells, for the broad range of ecosystem services they provide (including biofiltration, bioturbation of sediments, nutrient cycling and storage, habitat/habitat modification, environmental monitoring, food for other species, food for humans, products from shells such as jewelry, cultural value, existence value; see Vaughn 2017 for review) and for the cost to replace them if they are destroyed by a chemical spill or other anthropogenic disturbance (Southwick and Loftus 2017). Due to the high number of endangered species that occur in the Clinch River, and because the waterway is a designated mussel sanctuary in Tennessee, it is currently illegal to harvest mussels from the river in either Tennessee or Virginia. Therefore, no legal commercial market exists to put a dollar value on the mussel resource at PI. Moreover, while ecosystem services provided by mussels are likely substantial—increased productivity of benthic communities, sequestration of excess nutrients and contaminants, and food resources provided to both commercially and recreationally valuable fishes and other animals—the dollar values per type and unit of service are not available yet for mussels. For example, ecosystem services provided by healthy oyster reefs, excluding oyster harvesting, have been valued at $5,500 to $99,000 per hectare per year (Grabowski et al. 2012), yet corresponding estimates of the dollar value per hectare per year of a healthy mussel bed have not been established. Although we are unable to place a dollar value on the ecosystem services that could be provided by restored mussel assemblages, we can make attempts to estimate their replacement costs, for example, the cost to produce them at a hatchery to a size suitable for stocking (typically 20–30 mm and 1–3 yr old). Currently, prices range between $25.97 to $129.30 per mussel, depending on the ease or difficulty in producing individuals of a species (Southwick and Loftus 2017). Thus, just the replacement costs to return mussel populations to baseline levels at PI—not considering the value of lost ecosystem services—would easily be in the tens of millions of dollars.

SUMMARY AND CONCLUSIONS

Collection of long-term quantitative density data over the last 35 yr (1979–2014) has been critical to determining assemblage-level and population-level Clinch River mussel density trends in Tennessee and Virginia. It is now clear that the mussel assemblage in Tennessee has increased in density over this period and has stabilized at a mean density of $\sim$29/m^2. The long-term monitoring data collected in Tennessee can serve as a baseline to judge species recovery and restoration efforts in upstream reaches of the Clinch River in Virginia and in other streams throughout the Tennessee River drainage. The mussel fauna at PI has declined by 96% from its historically documented baseline density of 25/m^2 in 1979 to its current density of $\sim$1/m^2. It is possible that the significant increase in density at PI we observed from 2009 to 2014 represents natural recovery at the site. However, future sampling will be needed to confirm if this increase in density is a true upward trend. The lost mussel abundance and ecosystem services at the site represent more than a million mussels and tens of millions of lost mussel service years. Recovery of the assemblage to baseline or higher densities likely will take decades and will require active restoration of the fauna and their habitat. With exception of the presumed extinct *Epioblasma gubernaculum*, species extirpated from PI could be restored to the site using population sources downstream in the Tennessee section of the river and from other rivers. However, if water and sediment quality remain poor and do not improve over time, natural recovery and active restoration of the mussel assemblage at PI and nearby sites may not be possible for decades and could represent a permanent loss of ecological integrity and ecosystem services in the Clinch River.

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Appendix

Table A1. Counts of live mussels per species collected in the Clinch River at Pendleton Island, Scott County, Virginia, during qualitative surveys conducted from 1994 to 2016. Sample data are from [1]The Nature Conservancy unpublished data of survey of shell middens at Pendleton Island in 1994, [2]Neves and Beaty (1996), [3]Beaty and Neves (1997), [4]Beaty and Neves (1998), [5]Jones and Neves (1999), [6]Ahlstedt et al. (2005), [7]Jones and Beaty unpublished data (2014), and [8]Jones and Beaty unpublished data (2016).

Species	1994[1]	1996[2]	1997[3]	1998[4]	1999[5]	2004[7]	2014[7]	2016[8]
(1) *Actinonaias ligamentina*	51	51	81	77	95	138	107	214
(2) *Actinonaias pectorosa*	14	59	19	33	56	126	28	131
(3) *Alasmidonta marginata*	0	0	0	0	0	0	0	0
(4) *Amblema plicata*	21	140	78	35	68	88	21	66
(5) *Cyclonaias pustulosa*	0	0	0	0	0	0	0	0
(6) *Cyclonaias tuberculata*	3	10	16	9	12	37	18	36
(7) *Cyprogenia stegaria*	0	0	0	0	0	0	0	0
(8) *Dromus dromas*	0	0	0	0	0	0	0	0
(9) *Elliptio crassidens*	0	0	0	0	0	0	0	0
(10) *Eurynaia dilatata*	14	1	0	2	0	0	7	31
(11) *Epioblasma brevidens*	0	0	0	0	0	0	0	2
(12) *Epioblasma capsaeformis*	0	0	0	0	0	0	0	0
(13) *Epioblasma gubernaculum*	0	0	0	0	0	0	0	0
(14) *Epioblasma triquetra*	0	0	0	0	0	0	0	1
(15) *Fusconaia cor*	6	2	3	3	0	6	0	1
(16) *Fusconaia cuneolus*	17	8	2	2	4	3	1	2
(17) *Fusconaia subrotunda*	6	25	17	56	44	10	3	7
(18) *Hemistena lata*	0	0	0	0	0	0	0	0
(19) *Lampsilis abrupta*	0	0	0	0	0	0	0	0
(20) *Lampsilis fasciola*	7	0	0	1	0	14	4	4
(21) *Lampsilis ovata*	2	0	11	2	0	1	1	0
(22) *Lasmigona costata*	2	0	6	3	6	0	1	2
(23) *Lemiox rimosus*	0	0	0	0	0	3	0	0
(24) *Leptodea fragilis*	0	0	0	0	0	0	0	0
(25) *Ligumia recta*	2	0	2	0	1	0	0	1
(26) *Margaritifera monodonta*	0	0	0	0	1	0	0	0
(27) *Medionidus conradicus*	1	0	0	0	0	0	0	2
(28) *Plethobasus cyphyus*	1	2	0	1	0	3	1	0
(29) *Pleurobema cordatum*	0	0	0	0	0	0	0	0
(30) *Pleurobema oviforme*	5	1	6	0	1	0	1	0
(31) *Pleurobema rubrum*	1	0	0	0	0	0	0	0
(32) *Pleuronaia barnesiana*	0	3	0	2	0	0	0	0
(33) *Pleuronaia dolabelloides*	2	0	0	8	6	0	0	0
(34) *Potamilus alatus*	3	23	18	9	0	0	0	0
(35) *Ptychobranchus fasciolaris*	2	8	5	8	5	16	15	66
(36) *Ptychobranchus subtentus*	0	0	5	3	0	6	0	5
(37) *Strophitus undulatus*	0	0	0	0	0	0	0	0
(38) *Theliderma cylindrica*	5	0	1	0	3	1	0	1
(39) *Theliderma intermedia*	0	0	0	0	0	0	0	0
(40) *Theliderma sparsa*	0	0	0	0	0	0	0	0
(41) *Truncilla truncata*	0	0	0	0	0	0	0	0
(42) *Venustaconcha trabalis*	0	0	1	0	0	0	0	0
(43) *Villosa fabalis*	0	0	0	0	0	0	0	0
(44) *Villosa iris*	10	0	0	0	0	2	7	17
(45) *Villosa vanuxemensis*	4	0	1	0	0	1	1	1
Totals	179	333	272	254	302	455	216	590
Number of species (29)	22	13	17	17	13	18	15	19