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Spatio-temporal patterns of the decline of freshwater mussels in the Little South Fork Cumberland River, USA

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Abstract. The Little South Fork Cumberland River, Kentucky and Tennessee, USA, was a globally important conservation refugium for freshwater mussels (Mollusca: Unionidae) because it supported an intact example (26 species) of the unique Cumberland River mussel fauna including imperiled species. We used previous surveys and our 1997–1998 survey to reconstruct the historical fauna, to describe spatio-temporal patterns of density and number of species, and to evaluate the probable sequence and cause of observed mussel declines. We were specifically interested in better understanding how mussel assemblages respond to chronic disturbances, and how these changes manifest in persistence patterns. Density and numbers of species declined steadily from 1981 to 1998, but declines occurred first in the lower river (early 1980s), followed by declines in the upper river (late 1980s to early 1990s). Of the total species recorded from the Little South Fork, 17 (65%) are seemingly extirpated and five others appear near extirpation. Declines are associated with at least two, temporally distinct major insults. Lower river declines are associated with surface mining, whereas, oil extraction activities are implicated in upper river declines. Regardless of causal factors, species persistence was primarily a function of predecline population size with only the most numerous and widespread species surviving. At this time, the river appears lost as a conservation refugium for mussels despite its remoteness, predominantly forested watershed, and several layers of existing statutory and regulatory environmental safeguards. We suggest that the river could be restored and mussels reintroduced if an interagency task force is formed to identify and mitigate specific stressors now affecting most mussel species in the river.

Nomenclature: Turgeon et al. (1998).

Introduction

The Cumberland River system of Kentucky and Tennessee, USA, supports one of the most globally diverse freshwater mussel faunas (at least 87 species) of any similar-sized stream system and includes a number of endemic species (Cicerello et al. 1991; Parmalee and Bogan 1998). In the past 75 years, this fauna experienced a drastic decline in distribution, diversity, and density. The American Fisheries Society considers over half of the fauna (48 species) imperiled (Williams et al. 1993), and stream reaches supporting relatively intact mussel assemblages are few and widely scattered.

Until recently, the Little South Fork of the Cumberland River, Kentucky and Tennessee, supported one of the most important and intact mussel assemblages in the system. This fauna was composed of at least 26 native species, including two species protected under the U.S. Endangered Species Act (littlewing pearlymussel, *Pegias fabula*, and Cumberland bean, *Villosa trabalis*), a candidate for federal protection (fluted kidneyshell, *Ptychobranchus subtentum*), and 10 other mussel species considered imperiled throughout their range (Williams et al. 1993). The Little South Fork also supported a diverse fish fauna (Burr and Warren 1986) and, in general, was considered one of the highest quality upland stream systems in the southeastern United States (Starnes and Starnes 1980). However, beginning in the early 1980s, drastic mussel declines were documented in the lower Little South Fork (Anderson et al. 1991), and the future of the stream as a mussel refugium for the Cumberland River system was uncertain.

The recognized conservation importance of the Little South Fork and concern over apparent declines in the mussel fauna prompted a number of detailed mussel surveys beginning in the late 1970s. Consequently, the distribution and density of the stream's mussel fauna during the last 20 years is unusually well documented. We combined this information with results from a 1997–1998 survey to construct a detailed history of mussel declines in the Little South Fork.

Declines in small river mussel faunas of North America are increasingly common (e.g., Houp 1993; Houselet and Layzer 1997; Fraley and Ahlstedt 2000), but documentation is usually based on presence–absence data, limiting power to detect change (Strayer 1999; Strayer and Fetterman 1999; Vaughn 2000). Notably, little attention has been given to patterns of persistence after mussel declines in small rivers, even though at least some mussel species have persisted in most, if not all, streams that have experienced declines. Better understanding of these patterns can help identify and prioritize conservation action for species and their habitats.

To address these issues, we reconstructed the historical assemblage structure (richness, abundance) along the entire mainstem of the Little South Fork and examined temporal and spatial changes in the number of species and density over the period from 1977–1999. We then used these data sets (1) to evaluate the probable sequence and causes of changes in four segments of the river, and (2) to examine patterns of species persistence in the river. Specifically, we tested the hypothesis that persistence of a species was related to its historical abundance and distribution in the river. Finally, we assessed the Little South Fork in the context of conservation of the Cumberland River system mussel fauna.

Study area and history of the fauna

Study area

The Little South Fork is located on the Cumberland Plateau of the Appalachian Plateaus Physiographic Province in southeastern Kentucky and northeastern Tennessee, USA (Figure 1). The river originates in Pickett County, Tennessee, and

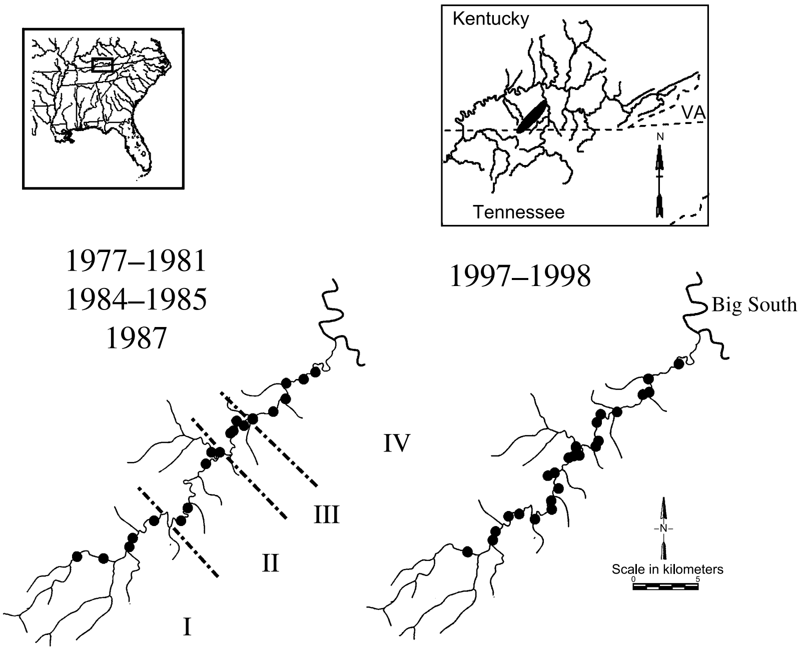

Figure 1. Previous (left) and recent (right) freshwater mussel survey localities (solid circles) in the Little South Fork Cumberland River, Kentucky.

continues northeastward into Kentucky (Wayne and McCreary counties) for about 69 river-km, where it enters an impounded section of the Big South Fork Cumberland River (Lake Cumberland reservoir). The stream is fourth order in size and drains a rugged, highly dissected area of about 298 km^2. Pennsylvanian sandstones cap the ridge tops, and Mississippian limestones underlie the lower slopes, valley floor, and streambed; karst features (e.g., caves, sinkholes) are common. Most tributaries do not flow in summer, but inflow from springs and groundwater upwelling is common along the entire river, and the river's flow is wholly or partly subterranean in a few short sections (Starnes and Bogan 1982). About 65–75% of the watershed is forested, but agriculture (primarily pasture) is practiced on the narrow floodplain and lower valley slopes. The downstream third of the watershed contains coal deposits below the ridge tops; surface mining of these deposits began in the mid-1970s and continued through the 1980s. The upstream portion of the watershed has several oil and gas fields that were first developed in the early 1900s (Munn 1914; Taylor 1977), but extraction was ongoing during our survey. The Little South Fork is mostly free-flowing, but Lake Cumberland reservoir, completed in 1950, embays the downstream-most 5 km. The reservoir precludes natural colonization of the Little South Fork by most riverine mussel species that occur in the upper Big South Fork or other Cumberland River tributaries.

The Little South Fork is protected by several layers of statutory and regulatory mandates. Two mussel species and one fish, the palezone shiner (*Notropis albizonatus*)

(Warren et al. 1994), are protected under the U.S. Endangered Species Act. The lower 16.7 river-km of the Little South Fork are designated under state law as a Kentucky Wild River and classified as an Outstanding Resource Water and Exceptional Water under the U.S. Clean Water Act. Flint Fork, a headwater tributary to the Little South Fork, originates in the Pickett State Forest which is managed by the state of Tennessee. In addition, the river mainstem forms the western proclamation boundary of the Daniel Boone National Forest with federal ownership confined primarily to the ridge tops that define the eastern divide and small tracts within the watershed. Surface mining in the watershed is regulated under the U.S. Surface Mining Control and Reclamation Act and oil extraction by state statutes, both of which are enforced by the Kentucky Department of Mines and Minerals.

History of the fauna

The Little South Fork is exceptional among rivers of the United States because both the distribution and density of its mussel assemblage has been well documented over the last 20 years. From 1977 to 1981, initial surveys were conducted along the length of the Little South Fork (Millican Associates, Inc. 1982; Starnes and Bogan 1982). Prompted by information of possible declines (Ahlstedt 1986; Ahlstedt and Saylor 1995–1996), a 1987 resurvey of freshwater mussels in the Little South Fork revealed a massive mussel die-off in the downstream third of the river (Anderson et al. 1991). The die-off was associated with establishment (ca. 1974) and subsequent expansion of coal surface mines in the lower river, but the habitat and mussel assemblage upstream of the mining impacts appeared unaffected (Anderson et al. 1991). The unimpacted, upstream mainstem of the river was considered a source of colonists for recovery of downstream mussel populations if conditions improved. The upper river was considered a significant refugium for imperiled and endemic mussels, as well as a source for reintroduction of species (via translocation or propagation) into their former ranges elsewhere in the Cumberland basin.

Methods

Sampling live mussels

We sampled a total of 29 sites located along 47 river-km of the Little South Fork (Figure 1) in July 1997 and August 1998. We sampled 23 sites to estimate mussel densities (269.5 m^2 total area sampled) and six sites to augment species richness estimates using visual searches. We surveyed collection sites of previous workers (Starnes and Bogan 1982; Millican Associates Inc., 1982; Anderson et al. 1991; Layzer and Anderson 1992; Ahlstedt and Saylor 1995–1996) and previously unsurveyed reaches. We selected previously unsurveyed reaches by using sites selected systematically (via a random start) for fish surveys (Poly 1997; Henry et al. 1999; and field notes). Reaches were delineated by the boundaries of habitat units (riffle or run). A complete list of sampling localities is available from the authors (Warren et al. 1999).

At each site, we sampled two to five 5 m × 0.7 m transects (7.0–17.5 m^2) in a habitat unit to estimate mussel densities. Generally, if two or three transects revealed no or few live mussels, we discontinued sampling within that habitat unit. We placed transects by laying a tape marked at 1 m intervals parallel to the stream channel, and using a random numbers table, randomly selected the longitudinal (upstream to downstream) and transverse (right, left, or middle of channel) positions of transects. We marked transect positions with anchored 5 m lines placed at a slight diagonal to the shore. We searched transects in 0.5 m^2 sections using a quadrat frame as a guide. Within each section, we searched by visually examining the substrate using a mask and snorkel or a glass-bottomed view bucket, disturbing the substrate to a depth of about 10 cm to dislodge buried mussels, and looking underneath large, flat rocks. We conducted visual searches similarly, but in order to cover larger areas, we did not extensively disturb the substrate. We identified and measured (total length, nearest 1.0 mm) all live mussels encountered and then replaced specimens in the substrate. In our August 1998 field survey, we examined females of three sexually dimorphic species (*V. taeniata*, *Villosa iris*, and *Lampsilis fasciola*) for gravidity of the gills. We classified reproductive condition of females as gravid, partially spent, recently spent, or not gravid. We inspected length-frequency histograms for common species represented in our transect samples to evaluate recent recruitment among segments; we summarize these for the upper and lower river as individuals less than or exceeding 50 and 40 mm in length. Because of the small adult size and resulting narrow length range of *Medionidus conradicus*, we excluded this species from length-frequency comparisons.

Sampling relict shells

At selected sites along the entire mainstem, we collected all relict mussel shells from shorelines, the streambed, and old muskrat feeding stations, to compare historical and present-day mussel faunas. We defined relict shells as those in which the nacre on the interior of the shell was weathered and no longer lustrous; these shells represent animals that died about 5 or more years prior to collection. Because of the abundance of limestone in the Little South Fork basin, waters are well buffered and mussel shells remain intact for long periods after death of the animal. Although estimates of diversity and abundance obtained from relict shell collections likely are biased against small and thin-shelled species, most species in the Little South Fork have relatively thick, resistant shells, and these collections provide a valuable record of the historical fauna. We bagged all relict shells in the field and identified them later in the laboratory. We excluded recently dead shells with lustrous nacre from counts.

Historical reconstruction and analysis

We compared temporal and spatial changes in density and number of species using surveys from 1977 to 1981 (Starnes and Bogan 1982), 1984–1985 (Ahlstedt and

Saylor 1995–1996), 1987 (Anderson et al. 1991; Layzer and Anderson 1992), and 1997–1998. We refer to these as the 1981, 1985, 1987, and 1998 surveys, respectively. To summarize trends over the entire river, we aggregated data from individual survey sites into four river segments (listed upstream to downstream) (Figure 1): Segment I, upstream of State Highway 167 bridge (36°39′03″ N, 84°35′52″ W) to Green Ford; Segment II, Green Ford (36°40′50″ N, 84°43′37″ W) to Kennedy Creek; Segment III, Kennedy Creek (36°44′16″ N, 84°41′27″ W) to State Highway 92 bridge; and Segment IV, State Highway 92 bridge (36°45′27″ N, 84°40′20″ W) to downstream of Freedom Church Ford (36°48′25″ N, 84°35′52″ W). We refer to Segments I and II as the upper river, and Segments III and IV as the lower river. For our survey, we calculated mean density (±95% confidence interval) using transect densities from each respective segment ($n = 17$, 30, 14, and 16 transects for Segments I–IV, respectively). Density data were available for Segments III–IV for the 1981 survey and Segments II–IV for the 1987 survey. For 1981 data, we calculated the mean density for each segment from individual quadrat samples (0.1 m^2, $n = 30$ and 60 quadrats for Segments III–IV, respectively). Individual quadrat data (0.1 m^2) from the 1987 survey were unavailable, so we calculated mean density by averaging reported site densities within each segment but were unable to calculate meaningful confidence intervals. For presentation and comparison, we converted the means (±95% confidence intervals) of our survey and the 1981 survey to individuals m^{-2}. We estimated number of species per segment for each survey as the cumulative number of extant species in each respective segment. Historical number of species is the cumulative number (relict shells and living) that we encountered in each segment plus species recorded in other surveys. We calculated historical relative abundance (percent) from our relict shell collections ($n = 691$, 1192, 471, and 641 individuals for Segments I–IV, respectively). We also calculated pair-wise segment percent similarities (Pielou 1984) using relict shell numbers from each segment. We expressed relict shell density as the number of shells m^{-1} of stream searched to compare numbers among segments. To examine patterns of historical abundance, we correlated (Spearman's r) historical relative abundance of a species in a segment with the average historical relative abundance of that species in immediately adjacent segments. To examine patterns of persistence, we correlated (Spearman's r) average historical relative abundance and the number of segments in which a species persisted in 1998. To further explore persistence patterns, we used logistic regression to model the probability of persistence on historical relative abundance (SAS Institute 2000).

Results

Current and historical assemblages

We encountered nine living mussel species at low densities in 1997–1998 (Table 1). We found 165 live mussels in 77, 3.5-m^{-2} transects and 71 live individuals in visual searches. Mean overall density was 0.58 ± 0.27 individuals m^{-2}. Density and

Table 1. Species density (±95% confidence interval, m^{-2}), number of extant and historical species, and species loss (%) of freshwater mussels in four segments of the Little South Fork Cumberland River, Kentucky, USA, 1997–1998. Segments are listed from upstream (I) to downstream (IV).

Species	Segment			
	I	II	III	IV
Lampsilis fasciola wavyrayed lampmussel	<0.1	0.1 ± 0.10	<0.1	<0.1
Ptychobranchus subtentum fluted kidneyshell	<0.1	0.3 ± 0.20	0.2 ± 0.21	0.1 ± 0.11
Villosa taeniata painted creekshell	0.6 ± 0.47	0.5 ± 0.33	<0.1	–
Villosa iris rainbow	<0.1	<0.1	–	–
Actinonaias pectorosa pheasantshell	<0.1	–	–	<0.1
Pleurobema oviforme Tennessee clubshell	–	<0.1	–	–
Medionidus conradicus Cumberland moccasinshell	–	<0.1	<0.1	–
Ptychobranchus fasciolaris kidneyshell	–	–	–	<0.1
Potamilus alatus pink heelsplitter	–	–	–	<0.1
Density ±95% CI (m^{-2})	0.7 ± 0.50	0.9 ± 0.61	0.3 ± 0.27	0.2 ± 0.20
Number of transects (3.5 m^{-2} each)	17	30	14	16
Total extant species	5	6	4	5
Historical species richness	17	19	22	25
Species loss (%)	71	68	82	80

numbers of species declined steadily and dramatically from 1981 to 1998 (Figures 2 and 3). Mean overall density declined 88% from 1981 to 1998 (4.90 ± 1.67 individuals m^{-2} in 1981, 1.57 individuals m^{-2} in 1987). Overall species richness in the stream declined 65% from historical richness, and 53% from 1981 to 1998 (26 species historically, 19 extant in 1981, 12 extant in 1987). Live Asian clams (*Corbicula fluminea*) were common and widespread in all river segments in 1998. Freshly dead shells were rare in all segments (<5/site), and all recent muskrat middens that we observed were composed exclusively of Asian clams.

Historically, most species were widespread in the river, and relict shell abundance indicated high assemblage evenness within segments and high assemblage similarity among segments. Historical relative abundance of a species in a segment was correlated highly and positively with its historical relative abundance in immediately adjacent segments ($r = 0.78$, $p < 0.001$, $n = 83$), indicating similar representation of species among segments. Two to three species were dominant (>10% relative abundance) in each segment, but only one species exceeded 30% relative abundance in any segment (Table 2). Percent similarity of historical assemblages was >80% for all pair-wise segment comparisons.

Spatial patterns and timing of decline

Declines in density and numbers of species in the Little South Fork occurred unevenly over time and among river segments. In the lower river, density and numbers of species declined most precipitously between 1981 and 1987 (Figures 2

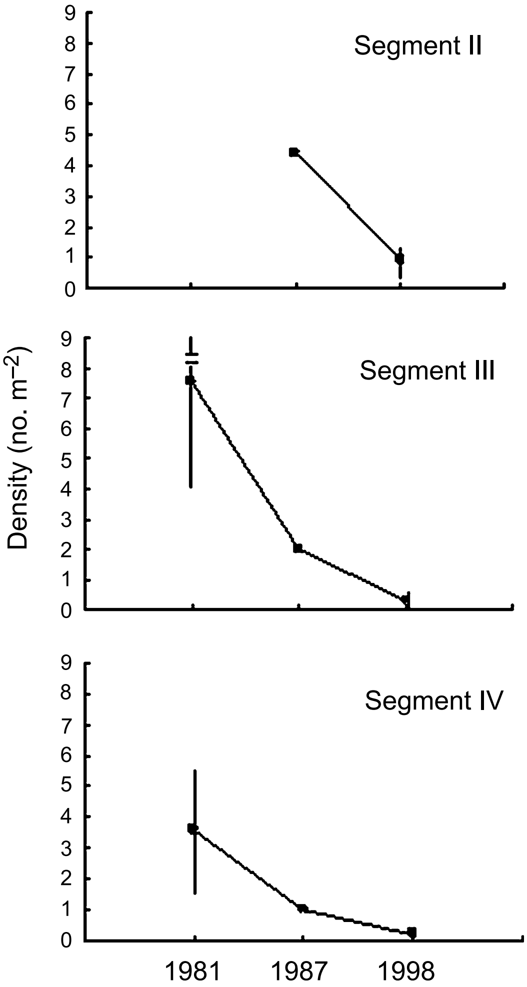

Figure 2. Changes in mean density of freshwater mussels from 1981 to 1998 in three segments of the Little South Fork Cumberland River, Kentucky. Vertical lines are 95% confidence intervals. Segment III upper confidence interval (11 m^{-2}) for 1981 is truncated.

and 3). High mussel densities and numbers of species were reported in 1981 (Starnes and Bogan 1982), but during and shortly after this time period, large numbers of freshly dead shells were reported at several lower river sites (Millican Associates, Inc. 1982; Ahlstedt and Saylor 1995–1996). Comparison of historical numbers of species with numbers observed in 1981 and 1985 shows that species loss began in the lower river even prior to these initial surveys (Figure 3), and by 1987, the mussel fauna of the lower river was all but eliminated.

In contrast, the upper river continued to support a diverse, dense fauna in 1987 (Figures 2 and 3). Density and numbers of species declined precipitously in Segment II between 1987 and 1998, but this segment retained the highest number

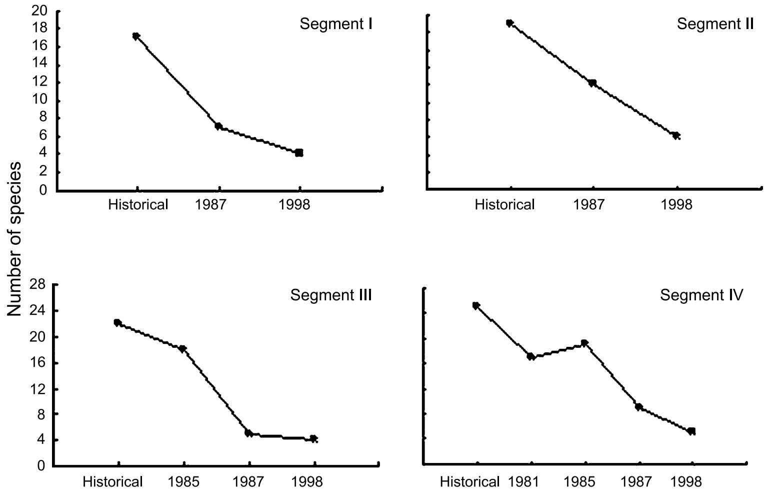

Figure 3. Changes in number of freshwater mussel species from 1981 to 1998 in four segments of the Little South Fork Cumberland River, Kentucky.

of species in 1998 and showed the lowest overall species loss of any river segment. The number of species declined by 66% in Segment I from 1987 to 1998. However, no density data exist for Segment I prior to 1998, or information on number of species in 1981, and we were unable to examine fully the timing or magnitude of the decline in this segment.

Relict shells also were distributed unevenly among segments in the Little South Fork. Although the lower river supported high densities of mussels in 1981, relict shells were rare in those segments in 1998 (0.4 and 1.0 shells m^{-1} in Segments III–IV, respectively). In contrast, relicts shells were abundant in the upper river in 1998 (1.5 and 1.9 shells m^{-1} in Segments I–II, respectively).

Although no small individuals of any species were taken in the river, evidence of the most recent recruitment was observed in the upper river. Throughout the river, most individuals (69%) averaged >50 mm total length. However, percentages of individuals <50 mm total length were much higher in the upper (35%) than lower (8%) river, and all individuals <40 mm total length occurred in the upper river (9 individuals, minimum = 34 mm total length). Sixteen gravid, partially spent, or recently spent *V. taeniata* (42–64 mm total length) and one gravid *V. iris* (34 mm total length) were observed in upper river, and one recently spent *L. fasciola* (51 mm total length) in the lower river.

Patterns of persistence

The decline of the mussel assemblage of the Little South Fork occurred evenly across species. The species persisting in the Little South Fork in 1998 (Table 1)

Table 2. Historical distribution and abundance of freshwater mussel species in four segments of the Little South Fork Cumberland River, Kentucky, USA. Entries are percent relative abundances in relict shell collections; 'R' indicates the species was recorded from that segment in previous surveys or as relict shells, but abundance was not available. Segments are listed from upstream (I) to downstream (IV).

	Segment			
	I	II	III	IV
Extant species				
Lampsilis fasciola wavyrayed lampmussel	20	18	15	11
Ptychobranchus subtentum[a,b] fluted kidneyshell	8	13	9	12
Villosa taeniata painted creekshell	42	27	21	10
Villosa iris rainbow	7	3	1	3
Pleurobema oviforme[b] Tennessee clubshell	2	4	3	2
Medionidus conradicus[b] Cumberland moccasinshell	3	4	3	3
Ptychobranchus fasciolaris kidneyshell	3	9	15	11
Potamilus alatus pink heelsplitter	R	2	11	17
Actinonaias pectorosa[b] pheasantshell	<1	–	–	17
Extirpated species				
Alasmidonta viridis[b] slippershell mussel	1	<1	<1	R
Elliptio dilatata spike	<1	<1	<1	6
Lampsilis cardium[b] plain pocketbook	2	3	3	4
Lasmigona costata flutedshell	1	1	10	5
Obovaria subrotunda[b] round hickorynut	2	7	4	7
Strophitus undulatus creeper	R	R	R	R
Toxolasma lividus[b] purple lilliput	3	2	3	2
Villosa trabalis[a,b] Cumberland bean	8	6	2	2
Ligumia recta[*,b] black sandshell	–	<1	–	–
Pegias fabula[a,b] littlewing pearlymussel	–	1	<1	<1
Utterbackia imbecillis paper pondshell	–	R	R	R
Alasmidonta marginata[b] elktoe	–	–	<1	<1
Leptodea fragilis fragile papershell	–	–	R	<1
Pyganodon grandis giant floater	–	–	R	R
Villosa lienosa little spectaclecase	–	–	R	<1
Actinonaias ligamentina mucket	–	–	–	<1
Cyclonaias tuberculata[b] purple wartyback	–	–	–	R
Historical species richness	17	19	22	25

*Not reported in previous surveys. Represented as a single relict shell in our survey.
[a]Endangered, threatened, or candidate status under the U.S. Endangered Species Act.
[b]Endangered, threatened, or of special concern status by the American Fisheries Society (Williams et al. 1993).

were the most widespread and abundant mussels in the historical assemblage (Table 2). Of nine surviving species (Table 1), seven were among the most abundant species in relict shell collections (>9%), and eight were present in all four segments (Table 2). In contrast, the 17 species not found alive showed low relative abundances in relict collections (most $\ll$10%), and nine of these species were restricted to $\leq$3 segments. The number of segments in which a species persisted was correlated positively with its mean historical relative abundance ($r = 0.75$, $p < 0.0001$, $n = 26$), indicating a strong link between present distribution and historical abundance. Logistic regression, modeling the probability of persistence on historical relative abundance, yielded a significant positive model with a good fit ($a = -3.57$, log likelihood $\chi^2 = 29.67$, $p < 0.0001$, $b = 0.37$, log likelihood $\chi^2 = 19.62$, $p < 0.0001$, Hosmer and Lemeshow Goodness-of-fit $\chi^2 = 4.77$, $p < 0.3114$, 87% of observations correctly classified). Adjusted odds-ratios indicated that the probability of persistence increased by a factor of 6.2 (3.07–15.87, 95% confidence interval) for each 5% increase in historical relative abundance.

Discussion

Current state of the fauna

The Little South Fork supported a globally important freshwater mussel assemblage late into the 20th century. The stream contains extensive areas of optimal habitat that once supported large populations of mussel species characteristic of medium-sized to headwater streams. Although, isolated in 1950 by construction of Wolf Creek dam, the fauna survived relatively intact for over 30 years after dam closure and likely would have been viable long into the future in the absence of additional insults. Instead, the fauna underwent rapid, extensive declines in about 20 years. Of the total species recorded from the Little South Fork, 17 (65%) seemingly are extirpated and five others approach extirpation. Extirpated species included two species protected under the U.S. Endangered Species Act, the littlewing pearlymussel (*P. fabula*) and Cumberland bean (*V. trabalis*). *P. fabula* historically occurred in numerous upper Tennessee and Cumberland river tributaries (Cicerello et al. 1991; Parmalee and Bogan 1998). By 1980, the *P. fabula* population in the Little South Fork was considered the largest extant population (Starnes and Starnes 1980; Starnes and Bogan 1982), and the lower river was regarded as essential conservation habitat for the species (Ahlstedt and Saylor 1995–1996). Loss of *P. fabula* from the Little South Fork reduces the number of extant populations to five or fewer, only one of which is likely viable (Ahlstedt and Saylor 1995–1996; S. Ahlstedt, personal communication). Similarly, *V. trabalis* was common historically in Cumberland River tributaries (Neel and Allen 1964), but loss of the species in the Little South Fork leaves only four extant populations, three in Cumberland River tributaries and one in a Tennessee River tributary (S. Ahlstedt, personal communication). Overall, loss of the river as a conservation refugium resulted in the loss of populations of at least nine mussels of global conservation significance.

Present low densities and restricted distributions portend low probability of long-term viability for all mussel species persisting in the Little South Fork. The Tennessee clubshell (*Pleurobema oviforme*), pheasantshell (*Actinonaias pectorosa*), kidneyshell (*Ptychobranchus fasciolaris*), and pink heelsplitter (*Potamilus alatus*) were extremely rare in the river, each being represented by only one or two living individuals. The Tennessee clubshell and pheasantshell have declined throughout their ranges (Williams et al. 1993). The painted creekshell (*V. taeniata*), rainbow (*V. iris*), wavyrayed lampmussel (*L. fasciola*), Cumberland moccasinshell (*M. conradicus*), and fluted kidneyshell (*P. subtentum*) may persist in the river. These were the most numerous species encountered, and females of some were gravid. Nevertheless, low densities of these species indicated small population sizes. For most species, recovery by natural recolonization is precluded because the river is isolated from source populations by Lake Cumberland reservoir.

Causes of decline and patterns of persistence

The decline of the mussel fauna in the Little South Fork from 1981 to 1998 occurred in a curious, downstream to upstream progression. This progression is supported strongly by temporal patterns in the decline of density and number of species during this period. The rarity of relict shells in the lower river contrasted with their abundance in the upper river also indicates that most animals in the lower river died well before those farther upstream. Shells of individuals in the lower river had mostly disintegrated by 1998. Finally, length frequencies indicate that conditions for reproduction and recruitment occurred most recently in the upper river, even though those conditions were apparently eliminated in the entire river by 1998. The downstream to upstream pattern in decline might suggest a pathogen has progressed upstream via a motile, intermediate host or other vector. Although we cannot dismiss this as a factor in the decline, we know of no other evidence suggesting the presence of a pathogen affecting mussels in the Little South Fork or any other small river. We compiled strong evidence, however, indicating that two temporally distinct insults related to resource extraction may have been responsible for the observed pattern of mussel declines in the river.

In the lower river, mussels were eliminated in synchrony with downstream to upstream expansion of coal surface mining along ridges of the lower river valley from the mid-1970s to mid-1980s (Anderson et al. 1991). As surface mining expanded during this period, mussel mortality events and decreased densities were observed in the mainstem, downstream of the mouths of tributaries draining newly mined areas (Millican Associates, Inc. 1982; Ahlstedt 1986; Anderson et al. 1991; Ahlstedt and Saylor 1995–1996). Surface mines were scattered along ridge tops across the lower river valley by the late 1980s, and mussels were largely eliminated in the lower river. Although precise stressors were not identified, high metal concentrations in sediments, ferric precipitates (‘yellow boy’) to nearly a meter in depth, and low pH (<4) were reported in several tributaries (Anderson et al. 1991; Layzer and Anderson 1992; Henry et al. 1999), all of which strongly implicate surface mine runoff in the decline of mussels of the lower Little South Fork (Anderson et al. 1991).

The cause of the decline in the upper river is not attributable to surface mining. We observed no evidence in the field or on aerial photographs (taken March 1997, Microsoft® 2002) of surface mining in the watershed of the upper river. Other than localized impacts of cattle on riparian zones along short river reaches (usually <100 m), we saw little evidence of physical habitat degradation that could be associated with the extensive recorded decline. In fact, the upper river appeared to provide many kilometers of exemplary habitat for freshwater mussels. The only directly observed pollutants in the river were associated with oil extraction.

Oil extraction has occurred sporadically in the Little South Fork watershed for about 100 years (Munn 1914; Taylor 1977), and numerous observations show that oil extraction and related activities have had a prominent recent influence on the river, and likely are involved in mussel declines in the upper river. In Segment I in 1998, we observed a persistent, oily slick on the river surface and petroleum coating extensive reaches of the stream bottom, riparian vegetation, and a spring head and run. The petroleum appeared to emanate from springs (many sulfurous) and groundwater upwellings along the river (Henry et al. 1999). Similar observations were reported for the upper river in 1978 and 1979, and high chlorides (63–131 mg/l), indicative of brine wastes often associated with oil extraction, have been measured repeatedly in this section of the river (Harker et al. 1979, 1980; Layzer and Anderson 1992). In 1987, sediments throughout the river contained variable, but detectable, levels of hydrocarbon contaminants (Robison 1996) that are characteristic of streams affected by crude or refined petroleum (Keller et al. 1998). Mortality of adult freshwater mussels has been observed following oil spills in streams, but little is known of the long-term threat of sediment-sorbed oil contaminants on larvae, juveniles, or adults (Keller et al. 1998; Weinstein 2002). A sharp peak in oil drilling occurred in the watershed in the early to mid-1980s (Figure 4), shortly before the beginning of steep declines in the mussel assemblage of the upper river. Further, Segment I has the densest concentration of wells in the watershed with many of these wells located in close proximity to the river or its tributaries ($<$100 m) (Kentucky Geological Survey 2003). Wells in Segment II are also numerous but less concentrated, and few wells are located in the lower river (Kentucky Geological Survey 2003). From these observations, we conclude that the cause of the mussel decline in the upper river was presumably from chronic exposure to an as yet unidentified stressor(s) likely associated with ground- or surface-water contamination originating from well drilling or oil extraction.

A diverse mussel assemblage persisted in the Little South Fork until at least the late 1980s despite the long history of oil extraction in the watershed. In addition to the peak in oil drilling observed in the late 1980s, a peak of similar magnitude occurred in the early 1960s (Figure 4), and extraction activities also were intense after the initial opening of these oil fields in the early 1900s (Munn 1914; Taylor 1977). Two non-mutually exclusive scenarios may explain the seemingly long coexistence of mussels and oil extraction in the Little South Fork. First, the high numbers and concentration of wells drilled near the river during the 1980s would have increased the probability of river contamination and may have subjected the stream to more intense and sustained contamination than in previous periods of activity. Second, given the history of oil extraction in the watershed, it is likely that the stream has experienced intermittent, chronic oil-associated pollution for many years. During early extraction in the region, high volumes of brine water were pumped from wells (Munn 1914), much of which presumably entered nearby streams, and oil from new wells often flowed directly into streams with flows lasting for days (Jillson 1959). Poor well closure and maintenance continued to contaminate streams of the region well into the last century (Jillson 1959; U.S. Department of the Army 1976). However, before impoundment of the Cumberland

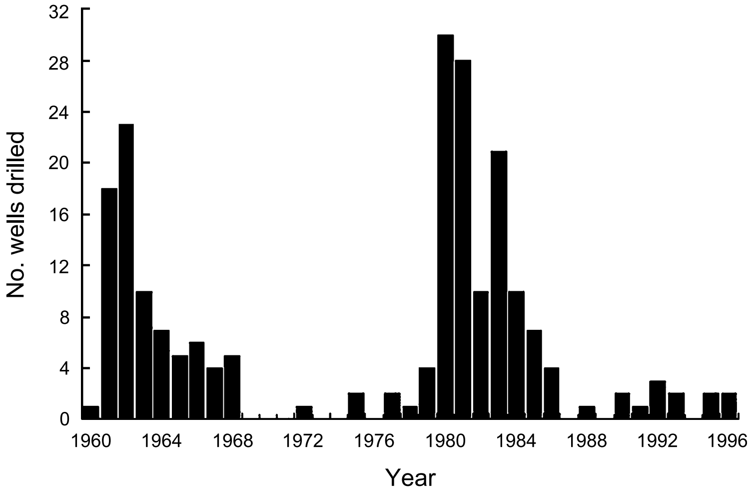

Figure 4. Number of oil wells drilled in the upper Little South Fork Cumberland River basin during the period of record of the Kentucky Geological Survey (1960–1996).

River in 1950, the Little South Fork could be recolonized from numerous mussel populations existing elsewhere in the Cumberland River system (Neal and Allen 1964). Even after 1950, but before the advent of surface mining in the lower watershed, reaches of the upper river impacted by oil pollution could be recolonized by large mussel populations in the lower river. The juxtaposition of severe insults to both the lower and upper river in rapid succession, as well as isolation of the river from source populations, finally eliminated the once considerable recovery capability of the Little South Fork mussel fauna.

Persistence patterns indicated that the causal factor(s) in declines in both the lower and upper river non-selectively affected all species. The association of historical abundance and present dispersion and the logistic model both supported our hypothesis that species persistence was related to historical population size. Our hypothesis was supported even though we indirectly measured population size, which suggests a strong operative effect. The relationship of population size to extirpation risk is a central tenet of conservation biology (Ricklefs and Miller 1999), but prevalence of presence–absence data on mussels in small rivers (Strayer 1999; Strayer and Fetterman 1999; Vaughn 2000) has precluded examination of the importance of population size on persistence. Although it is tempting to characterize persisting mussel species as 'tolerant' of chronic stressors, our results dispute such characterization. We hypothesize that the persistence pattern we observed is typical of mussel declines in many small rivers, particularly those affected by chronic disturbance (e.g. Houp 1993; Houp and Smathers 1995; Houselet and Layzer 1997; Fraley and Ahlstedt 2000). In these cases, species may differ in their 'tolerance' to changing stream conditions, but persistence will be primarily a function of their predisturbance population size.

Implications

The Little South Fork was a nationally and globally important conservation refugium for endangered species and for supporting a mussel assemblage representative of the diverse Cumberland River mussel fauna (Starnes and Bogan 1982; Schuster et al. 1989). The decimation of this important mussel refugium calls into question the adequacy of the environmental safeguards that are legislated to prevent such losses. The mussel assemblage of the Little South Fork was destroyed despite the river's remoteness, predominately forested watershed, and existing protective blanket of state and federal statutes, regulations, and management agencies. In response to mussel declines, the aquatic life use support designation recently was downgraded to 'Threatened' for the lowermost Little South Fork (Kentucky Division of Water 1998), but this occurred well after the demise of mussels in the lower river. No such designation has been forthcoming on the upper river. Clearly, an array of state and federal agencies have statutory and regulatory authority over the river and its organisms, but none of these protections in whole or in part mitigated the loss of one of the last mussel refugia in the Cumberland River drainage. The legacy of the Little South Fork mussel fauna is the outcome of competing interests of resource extraction and biodiversity conservation, coupled with trenchant institutional fragmentation of responsibilities for water-related resources (Noss and Cooperrider 1994). Avoidance of this kind of legacy is contingent upon increased coordination and communication among regulatory entities.

The Little South Fork still could serve as a viable reintroduction site for freshwater mussels in the future. The success of reintroductions of native mussels is contingent upon identifying problems in the river, and as possible, correcting factors that contributed to the observed mussel declines. Specifically, an interdisciplinary task force is needed to identify sources of funding to study and rehabilitate the watershed; to establish an interdisciplinary scientific investigation to identify surface and ground water contaminants and incidence of stress, disease, or toxic compounds in mussels; to initiate a landowner contact program to educate landowners on the ecological and water quality benefits of implementing best management practices in riparian areas (e.g., revegetation, fencing); and to revise recovery plans of endangered species to reflect loss of populations in Little South Fork and to evaluate the potential for reestablishment. Effective conservation of aquatic resources, such as in Little South Fork, will require oversight, regulation, and management that fully address the integral nature of land and water.

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