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[Article]

Effects of Severe Drought on Freshwater Mussel Assemblages

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Abstract.—We examined changes in freshwater mussel abundance and species composition at eight sites in Alabama and Mississippi in response to a severe drought in 2000. Five small-stream sites in Bankhead National Forest were heavily impacted by drought; one site dried almost completely, and four sites experienced total or near cessation of flow but retained water in their channels to a large extent. In contrast, three large-stream sites retained flow and experienced only minor streambed exposure, primarily along the stream margins. In small streams, overall mussel density before and after the drought declined by 65–83%, and the magnitude of the decline did not differ among streams regardless of whether the channel dried or remained wetted. Introduced *Corbicula fluminea* (Asian clam) experienced near total mortality and declined to a greater extent than native unionids. The magnitude of decline was similar among unionid species, and the likelihood of surviving the drought was mostly a function of predrought abundance; differences in drought tolerance among species were not evident. Consequently, assemblage composition changed primarily because of the loss of rare species, resulting in drainagewide homogenization and convergence on a shrinking species pool. In contrast, we found no evidence for changes in the total abundance or composition of mussel assemblages in large streams that continued to flow during the drought. Our results show that mussels are highly sensitive to the secondary effects of drought—most likely the low levels of dissolved oxygen caused by low flow, warm temperatures, and high biological oxygen demand—in addition to the direct drying of their habitat. The postdrought abundances of some species in Bankhead National Forest may now be below the minimum necessary for successful reproduction. These populations, which are isolated by reservoirs, may be in a downward spiral from which they will have difficulty recovering in the absence of immigration.

Like many other endangered organisms, remnant populations of freshwater mussels are often small and isolated from other populations. Some species survive as reproducing populations only in a single, short stream reach (e.g., Rogers et al. 2001), and many others are represented by a few small, widely separated populations (Shelton 1997; Parmalee and Bogan 1998; Jones et al. 2004; Warren and Haag 2005). Even in ostensibly well-protected conservation refuges, small refuge size and isolation render these populations highly vulnerable to extinction through loss of genetic variability, chance fluctuations in reproduction and survivorship, and environmental disturbance (Gilpin and Soule 1986).

Drought is one of the most pervasive forms of natural environmental disturbance in inland aquatic ecosystems, especially in small streams, but the generalized effects of drought on mussel communities are poorly understood. Previous workers considered freshwater mussels as a group well adapted to survive prolonged emersion (Byrne and McMahon 1994), but this generalization was based on results from a small number of wetland-adapted lowland species, which do not accurately represent the majority of the North American fauna. One species, *Uniomerus tetralasmus* (pondhorn), can persist in ephemeral wetlands by burrowing into the substrate (Frierson 1903) and can survive emersion for nearly 2 years (Holland 1991). Other lowland species, including *Toxolasma paulus* (iridescent lilliput), *T. texasiensis* (Texas lilliput), and *U. caroliniana* (Florida pondhorn), can survive moderate periods of emersion or low levels of dissolved oxygen (Holland 1991; Gagnon et al. 2004). In contrast, many riverine mussels and the introduced *Corbicula fluminea* appear to be intolerant of low dissolved oxygen and emersion, especially in warm temperatures (Holland 1991; Bartsch et al. 2000; McMahon 2001) and sustain high mortality when stranded in drying pools or on stream margins (Metcalf 1983). Mussels can move short distances to deeper water in response to receding water levels (Coker et al. 1921; White 1979). In large streams with permanent flow and resultant high levels of dissolved oxygen, this response probably decreases drought-associated mortality (Golladay et al. 2004). In small, shallow streams, the rarity of deeper refuges coupled with higher likelihood of low flows and low dissolved oxygen renders many mussel species vulnerable to emersion and other drought effects (Gagnon et al. 2004). Because mussel species occurring in different habitats may differ substantially in drought tolerance, context-

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TABLE 1.—Locations and characteristics of freshwater mussel sampling sites in Alabama and Mississippi. Link magnitude, a surrogate measure of watershed size, is the number of first-order stream segments upstream of the sampled reach as determined from U.S. Geological Survey 7.5′ topographic maps (see Haag and Warren 1998).

Stream	Sampling location	Latitude and longitude	Drainage area (km^2) (stream order; link magnitude)	Years	Area sampled (m^2)
Headwater streams in Bankhead National Forest, Alabama					
Brown Creek	Trail 223H crossing, 9.1 km ENE of Grayson, Lawrence County	34°18′20″N, 87°14′09″W	9 (III; 8)	1993	25.0
				2002	34.1
Brushy Creek	Forest Service road 254, 6.5 km NE of Grayson, Lawrence County	34°19′51″N, 87°17′09″W	24 (IV; 31)	1993	26.0
				2001	40.6
Flannagin Creek	Forest Service road 208 crossing, 9.1 km NW of Grayson, Lawrence County	34°20′20″N, 87°23′18″W	24 (III; 34)	1993	25.5
				2001	47.4
Rush Creek	Forest Service road 245 crossing, 10.4 km NW of Addison, Winston County	34°16′26″N, 87°15′06″W	30 (IV; 29)	1993	12.5
				2001	33.6
Sipsey Fork	Mouth of Hurricane Creek, 5.2 km SW of Grayson, Winston County	34°15′11″N, 87°22′02″W	267 (VI; 337)	1993	25.0
				2002	43.6
Large streams					
Little Tallahatchie River	Below Sardis Dam, 12.1 km SE of Sardis, Panola County, Mississippi	34°23′56″N, 89°47′25″W	4,002	1999	20.0
				2001	20.0
Sipsey River, site 1	0.4 km upstream from Greene County road 156 bridge, 19.5 km E of Aliceville, Pickens and Greene counties, Alabama	33°06′23″N, 87°56′50″W	1,729	1999	8.9
				2001	23.0
Sipsey River, site 2	0.9 km downstream from boat ramp along Greene County road 156, 22.7 km E of Aliceville, Pickens and Greene counties, Alabama	33°07′18″N, 87°54′38″W	1,765	1999	7.6
				2001	15.4

specific effects of drought on mussel assemblages remain poorly known.

The southeastern United States experienced a severe drought in 2000 (Golladay et al. 2004; Adams and Warren 2005). Streamflow declined to extremely low levels throughout Alabama and Mississippi, and many small streams dried completely, including streams that formerly supported diverse and abundant mussel assemblages. We examined the effects of the drought on mussels in a variety of environmental settings by comparing predrought and postdrought mussel abundance in five small streams in Bankhead National Forest and in two large streams elsewhere in the region. Our primary objectives were to (1) compare the effects of drought on mussels in streams of different sizes that experienced varying degrees of channel exposure, (2) determine the degree to which mussel species differed in their response to drought, (3) determine to what extent mussels were able to survive emersion in dewatered sections of stream, and (4) consider the potential long-term impacts of the drought on these mussel assemblages.

Study Area

Small streams.—We sampled five streams in Bankhead National Forest, Alabama, in 1993 (predrought) and again in 2001 or 2002 (postdrought). All sites were within one of the two major drainages in the forest, Brushy Creek (Brown Creek, Brushy Creek, and Rush Creek) and Sipsey Fork (Flannagin Creek and Sipsey Fork). The sites encompass a range of stream sizes that support mussels, from the largest streams (Sipsey Fork) to the smallest streams (Table 1; Haag and Warren 1998). These upland streams lie on the Cumberland Plateau and are typical for this physiographic province (Boschung and Mayden 2004), being located in deeply entrenched valleys and characterized by pool–riffle habitats with gravel, sand, slabrock, and bedrock substrates. Four of the streams (Brown, Brushy, Rush, and Sipsey) flow through Parkwood Formation shales and sandstones; the soils of this formation tend to be deep and moderately permeable and contribute to sustaining streamflow during dry periods (Mast and Turk 1999). Flannagin Creek flows through porous, fractured Bangor Limestone, which includes karst features; soils of this formation are significantly less permeable than soils elsewhere in the basin and contribute to the flashy nature of these streams (Mast and Turk 1999).

Bankhead National Forest is a globally important conservation refuge for mussel diversity (Master et al. 1998; Smith et al. 2002), supporting a fauna of at least

16 species (including 4 species protected under the U.S. Endangered Species Act) and the largest known populations of at least 3 species (Haag and Warren 1998; McGregor and Pierson 1999). The forest includes large, contiguous tracts of forested land that almost completely encompass the entire watersheds of the two major stream networks: Sipsey Fork (order VI) and Brushy Creek (order V). A large portion of the Sipsey Fork drainage is designated a federal wilderness area. However, mussel populations in the forest are fragmented and isolated by Lewis Smith Reservoir, a large (8,580 ha, >50 km long), deep, hypolimnetic storage reservoir that impounds extensive sections of the lower Sipsey Fork and Brushy Creek. This reservoir eliminates the interconnectivity of the upstream and downstream sections and of the two unimpounded upstream sections of Sipsey Fork and Brushy Creek, preventing the movement of most stream organisms between these two watersheds. The Brushy Creek watershed is also fragmented by Brushy Lake dam, which blocks movement of aquatic organisms between the upper and lower watershed. Therefore, despite the large size and inclusiveness of the forest, the mussel fauna in reality consists of a collection of small, isolated populations, all of which are highly vulnerable to regional and local disturbance.

Large streams.—In 1999 (predrought) and 2001 (postdrought), we sampled mussels at one site in Mississippi's Little Tallahatchie River (Yazoo River system) and two sites in Alabama's Sipsey River (upper Tombigbee River system; Table 1). The Sipsey River is distinct from the Sipsey Fork of the Black Warrior River system described previously. Both the Little Tallahatchie and Sipsey rivers are large streams occupying broad floodplains in the East Gulf Coastal Plain physiographic province, but other aspects of their physical habitats differ greatly. Flow at the Little Tallahatchie River site, located in Lower Lake immediately downstream of Sardis Reservoir, is regulated by a flood control release schedule from Sardis Dam and is further influenced by a low-head dam 2–3 km downstream of the study site (Haag and Warren 2007). Throughout most of its length, the Sipsey River is unregulated and unmodified, and the watershed is forested; consequently, water quality is high, and the river supports one of the most intact mussel assemblages in the region (McCullagh et al. 2002). Both streams flow through extensive alluvial deposits and sand and gravel sediments of Tertiary or Cretaceous origin.

Methods

Mussel sampling in small streams.—At each site within Bankhead National Forest, we established a sample reach about 300 m in length that included a variety of habitat types. Within the sample reach, we sampled two to five habitat units (riffles, runs, or shallow pools 7–65 m long); the number and length of the units sampled depended on the natural configuration of the reach. We did not sample habitat units predominated by bedrock or deep, sluggish pools because these habitats typically yield low numbers of mussels in this region. Bedrock substrates were common, but deep pools were absent at most sites. In predrought sampling, we sampled about fifty 0.5 m^2 quadrats at each stream site with the exception of Rush Creek, where we used 0.25 m^2 quadrats (Table 1). We placed quadrats by superimposing a grid consisting of 1-m^2 cells over each habitat unit and selecting 25% of the cells via a random number table. We placed a quadrat in the center of each chosen cell, and using mask and snorkel, we searched for mussels within the quadrat to an excavated substrate depth of about 15 cm. We identified, measured (longest anterior to posterior distance; nearest 0.1 mm), and released all live unionids encountered. We counted, but did not measure, all *Corbicula fluminea* encountered in quadrats at Flannagin Creek and Sipsey Fork, but we did not detect this species in Brown or Brushy creeks. *C. fluminea* was present at low to moderate densities in Rush Creek, but we did not begin counting this species until after Rush Creek sampling was completed.

After the drought we sampled the same stream reaches but used transects instead of quadrats to ease sample unit placement and increase sample unit size and thereby improve the precision of our density estimates. In each habitat unit, we sampled one transect for every 5 m of unit length. We determined the locations of each transect within the habitat unit by drawing a random number between 0 and the unit's length (m). The random number specified the distance from the downstream end of the unit to the location of the transect. At each selected point, we sampled a cross-sectional transect perpendicular to the stream channel using a 0.125-m^2 quadrat flipped end over end as a guide; the area of each transect was therefore 0.354 m times the width (m) of the stream at that point. At each site, we sampled more total area postdrought than predrought (Table 1).

Mussel sampling in large streams.—In Lower Lake of the Little Tallahatchie River, much of the habitat is relatively uniform, so we arbitrarily established the site boundaries (approximately 45 × 62 m) within a section of the stream known to harbor a diverse mussel fauna (Haag and Warren 2007). Before the drought, we took eight 2.5-m^2 samples arrayed in a grid across the study site. To increase sampling precision postdrought, we reallocated our effort by taking 10 systematic samples,

each consisting of eight sample points arrayed in a grid across the study area (Strayer and Smith 2003). At each point we sampled a single 0.25-m^2 quadrat, and we combined samples from the eight points to represent a single systematic sample of 2.0 m^2. We collected whole-substrate samples by excavating to a depth of about 15 cm using a diver-operated dredge. We transported samples to shore and retrieved mussels by washing the substrate across a series of three sieves (smallest mesh size = 2.5 mm).

In the Sipsey River, we established a 100-m reach (site 1) and a 60-m reach (site 2), each of which encompassed a riffle–run complex bordered upstream and downstream by deep, sluggish pools. We divided each reach along its length into 10 units of equal size. Within each unit, we sampled a single transect across the stream, beginning at a randomly chosen starting point and using a 0.125-m^2 quadrat flipped end over end as a guide. The area of each transect was 0.354 m times the width (m) of the stream at that point. We collected and processed samples via a portable dredge, as previously described.

Data analysis.—We examined the changes in mussel abundance and assemblage composition before and after the drought by using randomization procedures to avoid violating the assumptions of parametric tests (Manly 1997). Except where otherwise noted, we derived confidence intervals and *P*-values from 10^4 randomizations and computed all confidence intervals by using the percentile bootstrap (Dixon 2001). We analyzed the data for unionids and *Corbicula fluminea* separately and calculated mean overall mussel abundance (number of individuals per area [m^2] for all unionid species combined) and 95% confidence intervals for each site–year combination. We tested each site for differences in overall mussel abundance between years via a randomized one-way analysis of variance (ANOVA; Manly 1997). We also calculated the percent decline in abundance between surveys at each site and the 95% confidence limits around the estimated percent change.

We tested for species-specific responses to drought at each site in two ways. First, to account for different initial abundances among species, we conducted a randomized one-tailed paired *t*-test (Sokal and Rohlf 1995; Manly 1997) for each site to test the alternate hypothesis that mussel species overall were less abundant postdrought than predrought. Second, we used a randomized correlation (Pearson's product-moment correlation coefficient) at each site to test the hypothesis that the abundances of individual species in the community were associated before and after the drought.

We examined the changes in mussel assemblage composition among sites in the Sipsey Fork and Brushy Fork system (Bankhead National Forest) in two ways. First, we used multiresponse permutation procedures (MRPP; PC-ORD, McCune and Mefford 1999) with Euclidean distances to inferentially test the hypothesis of no mussel assemblage differences between years (155 samples × 15 species matrix grouped by year but excluding samples with no mussels). The MRPP is a nonparametric randomization analog of parametric procedures that is similar to discriminant analysis but with the advantage of not requiring distributional assumptions (Mielke and Berry 2001). Second, to visualize changes in assemblage composition, we factored principal components from the correlation matrix of individual species abundances (samples with mussels) for all sites predrought and postdrought. We plotted the centroid of principal component scores for each site × year combination (Moyle and Vondracek 1985; Haag and Warren 1998) and plotted vectors indicating direction and magnitude of change at sites after the drought. Because overall mussel abundance and species-specific abundance in both the Little Tallahatchie and Sipsey rivers changed little after the drought, we did not examine changes in mussel assemblage composition in detail at these sites.

Drought conditions.—We made observations of the physical conditions at all study sites at the lowest point of the drought on November 3, 2000, about 1 week before the onset of fall rains. Because Flannagin Creek dried almost completely, we measured and recorded the location of all remaining pools within the study reach at this stream. We obtained flow and water temperature information on the Sipsey Fork and Sipsey River from U.S. Geological Survey recording gauges (02450250 near Grayson, Alabama, and 02446500 near Elrod, Alabama; waterdata.usgs.gov/al/nwis). We obtained flow information on the Little Tallahatchie River (as discharge from Sardis Reservoir) from the Vicksburg District, U.S. Army Corp of Engineers, Vicksburg, Mississippi.

Results

Drought Conditions

As early as May 2000, the drought in northern Alabama and Mississippi was classified as "moderate," but dry conditions continued throughout the summer and from August 22 to October 31, 2000, the drought was classified as "exceptional," the most severe drought intensity category (corresponding to −5.0 or less on the Palmer Drought Index; U.S. Drought Monitor 2006). In the Sipsey River and Sipsey Fork, this drought resulted in mean monthly discharges far below long-term mean and median levels from May until November, and even in the regulated Little

Tallahatchie River, flow relative to historical flow was diminished from May to August until reservoir drawdown began in September (Figure 1). The Sipsey River experienced the longest period of sustained low flows since 1954, including the second lowest flows ever recorded for July and September. Sipsey Fork experienced the longest period of sustained low flows in the 35-year period of record (1966–2000), including the two lowest mean monthly discharges (October and September) ever recorded at the site for any month. Water temperatures from June to October were 2.0–2.6°C above average in the Sipsey River including the warmest August on record (29°C). In Sipsey Fork, water temperatures from June through August were 1.8–2.9°C above average including one of the two warmest Julys on record (26.5°C).

None of our large-stream study sites experienced extensive dewatering of the streambed and, although reduced, flow continued in both the Sipsey River and the Little Tallahatchie River throughout the drought (Figure 1). In the Sipsey River, shallow areas along the stream margin were dewatered. Dewatered areas that formerly supported abundant mussel populations were littered with hundreds of dead mussels that were unable to retreat to deeper water. However, such instances of high mortality were rare and dewatered sections of streambed represented a small percentage of the wetted streambed area.

The drought affected streams in Bankhead National Forest in different ways depending on their underlying geologic formations. Streams flowing through Parkwood Formation shales and sandstones (Brown, Brushy, Rush, Sipsey Fork) were extremely low by the end of the drought and experienced sharply reduced flow (Figure 1) characterized by slow, nearly imperceptible movement of interstitial water within riffle substrates and no flow in pools. However, all four streams maintained wetted channels except in the shallow areas along their margins. In areas with exposed streambed, the substrate remained moist with the water table near the surface. Even the smallest stream, Brown Creek, suffered little exposure of the streambed. Owing to early and heavy leaf fall induced by the drought, combined with low-flow conditions, the surfaces of streams were covered thickly with leaves, particularly in Brown and Brushy creeks.

The only stream in our study flowing through the Bangor Limestone formation, Flannagin Creek, was impacted by the drought to a greater degree than all other study streams. Even though Flannagin Creek is much larger than Brown Creek and comparable in size to Brushy and Rush creeks (Table 1), the channel was dewatered almost completely, and only isolated, small pools and moist areas remained in the streambed. In the

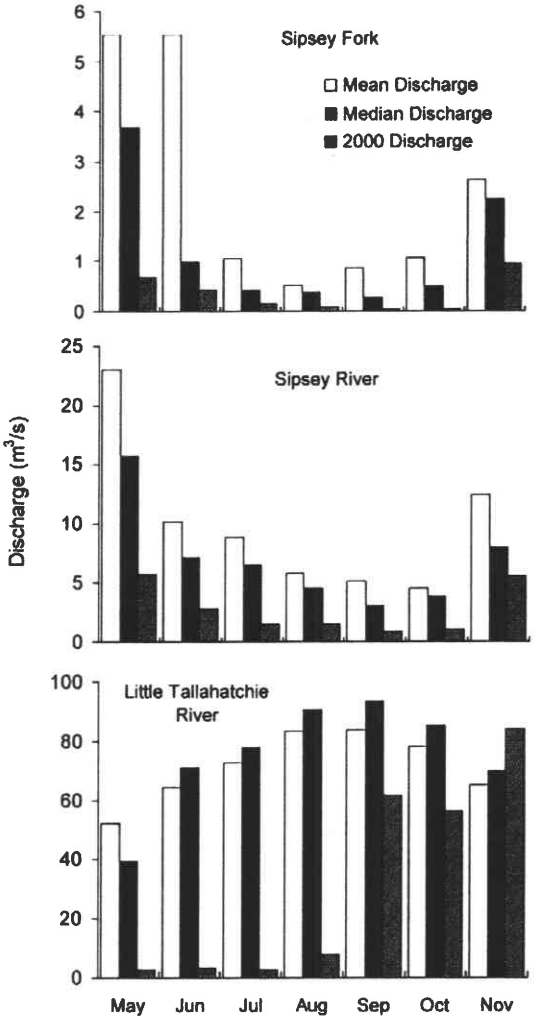

FIGURE 1.—Historical mean and median monthly discharges compared with the discharge in 2000 in two Alabama streams, Sipsey Fork (a small stream; 1966–2000) and the Sipsey River (a large stream; 1929–2000), and one Mississippi stream, the Little Tallahatchie River below Sardis Dam (a large stream; 1947–2005).

stream reach that we examined, 73% of the linear channel distance (428 of 584 m) was completely dry from bank to bank, and digging in the substrate in these areas produced no water or observable moisture at depths of at least 15 cm. In dry sections of the channel, we found numerous dead unionids including many paired valves in situ, representing individuals that had died in place in the substrate. We found no live mussels in the dry sections of the channel. Wet sections of the channel consisted of isolated small, shallow pools from 4 to 42 m long (mean = 13 m) and up to 1 to 2 m wide.

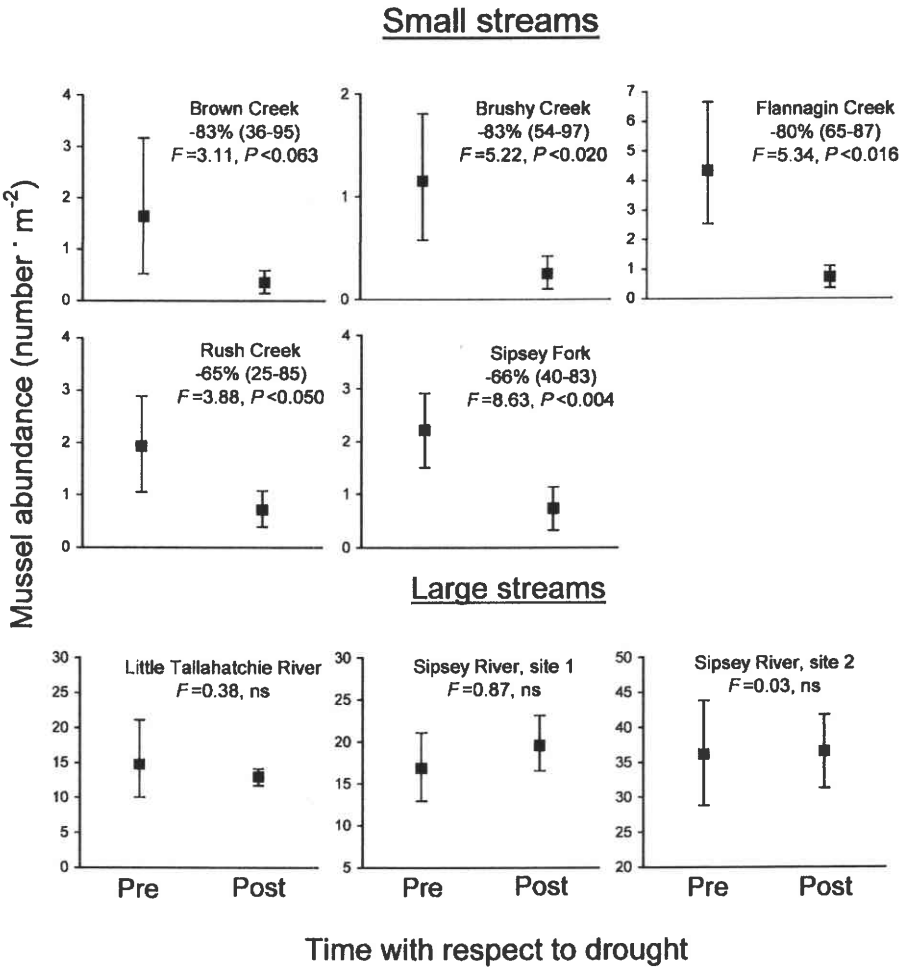

FIGURE 2.—Mean predrought and postdrought abundance of freshwater mussels at five small-stream sites (1993 and 2002) and three large-stream sites (1999 and 2000); the thin vertical lines represent the 95% confidence intervals of the means. The percentage declines (95% confidence intervals in parentheses) and the results of significance tests are given for the small streams; in the large streams there were no significant differences between predrought and postdrought abundance (ns; $P > 0.05$).

Drought Effects in Large Streams

Drought had no measurable effect on unionid assemblages in large streams. Unionid abundance did not change significantly predrought to postdrought at the Sipsey River sites or at the Little Tallahatchie River site (Figure 2). The abundance of *Corbicula fluminea* did not change at Sipsey River site 1 but increased significantly and by similar percentages at Sipsey River site 2 and at the Little Tallahatchie River site (Table 2). Unionid community composition was similar at all large-stream sites before and after the drought. Mean abundance across species did not change (paired *t*-tests; Tables 3, 4), and species abundances before and after the drought were highly correlated at all sites ($r = 0.97$–0.99, all $P < 0.0005$).

Drought Effects in Small Streams

In contrast to the large streams, unionid and *Corbicula fluminea* abundance in Bankhead National Forest declined precipitously as a result of the drought. The precision of our estimates of unionid abundance was low in predrought sampling because of small sample sizes and the highly patchy nature of mussel distribution (Figure 2). Nevertheless, overall unionid abundance was significantly lower at all sites except Brown Creek, which was marginally significant ($P < 0.07$), despite our low power to detect declines (Figure 2). The estimated declines ranged from 60% to 83% among all five sites, but the confidence intervals overlapped widely (Figure 2). Abundance of *C. fluminea* was also significantly lower postdrought in

TABLE 2.—Mean abundance (number/m^2) and, where significant, the estimated percent change in the abundance of *Corbicula fluminea* at two small-stream sites and three large-stream sites before and after the 2000 drought; 95% confidence intervals are in parentheses.

Stream	Predrought abundance	Postdrought abundance	Estimated change (%)
Small streams			
Flannagin Creek	30.2 (23.0–37.4)	0.7 (0.0–1.8)	−98 (−94 to −100)
Sipsey Fork	59.8 (50.9–69.2)	6.2 (4.1–7.5)	−90 (−87 to −93)
Large streams			
Sipsey River, site 1	20.4 (13.9–27.5)	19.2 (15.0–23.5)	
Sipsey River, site 2	16.6 (5.8–36.0)	52.4 (43.6–61.3)	216 (75–313)
Little Tallahatchie River	3.8 (1.6–6.7)	11.2 (9.8–12.6)	195 (103–270)

Flannagin Creek and Sipsey Fork. At both streams, the estimated percent decline was greater for *C. fluminea* than for unionids, and the confidence intervals around the estimated declines between *C. fluminea* and all other unionids did not overlap (Table 2; Figure 2).

In Flannagin Creek postdrought, live unionids and *Corbicula fluminea* were found only in sections of the channel that retained water at the lowest point of the drought. Concordant with our observations during the drought, we found large numbers of dead shells (including many paired valves oriented in situ in the substrate) but no live mussels in sections of the stream that were dry during the drought but had supported abundant mussel populations before the drought.

Species richness changed to a variable extent among streams but was generally similar from pre- to postdrought (Table 5). Richness was unchanged at Brown Creek and changed little at Brushy Creek, Rush Creek, and Sipsey Fork. The steepest decline in richness occurred at Flannagin Creek (predrought = seven species; postdrought = four species). In all cases, species that were not detected postdrought were rare before the drought ($\leq$0.16 individuals/m^2). All of the species detected alive in the forest before the drought were also detected after the drought, so that there was no loss of richness basinwide. *Potamilus purpuratus* (bleufer) was represented only as a single weathered shell before the drought but was not found after the drought. A single live individual of *Toxolasma corvunculus* (southern lilliput) was found after but not before the drought.

Several results indicate that all species were affected similarly by the drought. At all streams except Sipsey Fork, the three species with the highest rank abundances were the same before and after the drought (Table 5). In Sipsey Fork, the two most abundant species predrought *Ptychobranchus greeni* (triangular kidneyshell) and *Pleurobema furvum* (dark pigtoe) dropped in rank to a tied second owing to an apparent increase in the absolute abundance of *Villosa nebulosa* (Alabama rainbow). Most species declined by an estimated 63–100%, and this range contains the estimated overall unionid decline at all sites (Table 5; Figure 2). Except for *V. nebulosa* at Sipsey Fork, all species with estimated declines outside the 63–100% range or with estimated increases were rare (predrought abundances <0.16 individuals/m^2), yielding abundance estimates with poor precision. Mean abundance across species was significantly lower after the drought than before at all sites (paired *t*-tests; Table 5). Only 7 of 41 populations showed positive changes in abundance, but the magnitude of increase was small ($\leq$0.02 individuals/m^2) for all species except for *V. nebulosa* at Sipsey Fork (Table 5). Finally, individual species abundances before and after the drought were correlated significantly at all sites (r = 0.56–0.98, $P <$ 0.0038–0.049) except Brown Creek (r = 0.92, $P <$ 0.15), where power to detect association probably was low. Together, these results indicate that the drought

TABLE 3.—Changes in mussel abundance (number/m^2) by species in the Little Tallahatchie River before and after the drought of 2000. The test statistic t is for a one-tailed randomized paired *t*-test.

Species and statistic	Predrought	Postdrought	Difference
Amblema plicata	2.30	1.80	−0.50
Lampsilis cardium	0.10	0.00	−0.10
Lampsilis teres	0.05	0.04	−0.01
Leptodea fragilis	0.05	0.12	0.07
Obliquaria reflexa	1.55	1.20	−0.35
Plectomerus dombeyanus	0.00	0.04	0.04
Potamilus ohiensis	0.00	0.04	0.04
Potamilus purpuratus	0.00	0.32	0.32
Quadrula pustulosa	10.45	9.20	−1.25
Q. quadrula	0.05	0.12	0.07
Q. verrucosa	0.05	0.04	−0.01
Toxolasma texasisensis	0.10	0.00	−0.10
Truncilla donaciformis	0.00	0.04	0.04
Utterbackia imbecillis	0.05	0.00	−0.05
Mean			−0.128
t			−1.270
P			<0.122

TABLE 4.—Changes in mussel abundance (number/m^2) by species at two sites in the Sipsey River before and after the drought of 2000. Mussels reported only to genus were small specimens (<10.0 mm) that could not be identified to species. See Table 3 for further details.

Species and statistic	Site 1			Site 2		
	Predrought	Postdrought	Difference	Predrought	Postdrought	Difference
Amblema plicata	0.00	0.00	0.00	0.00	0.08	0.08
Elliptio arca	2.16	2.17	0.01	2.38	2.30	−0.08
E. crassidens	0.00	0.04	0.04	0.00	0.00	0.00
Fusconaia cerina	3.23	3.50	0.27	9.18	8.77	−0.41
F. ebena	0.00	0.00	0.00	0.20	0.00	−0.20
Hamiota perovalis	0.00	0.04	0.04	0.25	0.18	−0.07
Lampsilis ornata	0.46	0.43	−0.03	0.52	0.67	0.16
L. straminea	0.09	0.00	−0.09	0.00	0.00	0.00
L. teres	0.00	0.13	0.13	0.00	0.06	0.06
Lampsilis sp.	0.00	0.04	0.04	0.44	0.08	−0.36
Lasmigona complanata	0.00	0.05	0.05	0.00	0.00	0.00
Leptodea fragilis	0.00	0.04	0.04	0.00	0.12	0.12
Medionidus acutissimus	1.01	0.65	−0.36	1.62	0.68	−0.94
Megalonaias nervosa	0.00	0.00	0.00	0.00	0.26	0.26
Obliquaria reflexa	0.23	0.49	0.26	0.58	1.20	0.62
Obovaria unicolor	0.23	0.72	0.49	1.63	1.63	0.00
Pleurobema decisum	5.73	7.26	1.53	7.61	10.49	2.88
P. perovatum	0.11	0.00	−0.11	0.20	0.00	−0.20
Potamilus purpuratus	0.00	0.00	0.00	0.00	0.06	0.06
Quadrula asperata	2.26	2.62	0.36	5.60	5.34	−0.26
Q. rumphiana	0.21	0.23	0.02	4.00	3.88	−0.12
Q. verrucosa	1.04	0.94	−0.10	1.80	0.92	−0.88
Truncilla donaciformis	0.00	0.04	0.04	0.00	0.20	0.20
Villosa lienosa	0.09	0.13	0.04	0.10	0.00	−0.10
V. vibex	0.00	0.00	0.00	0.00	0.08	0.08
Villosa sp.	0.00	0.04	0.04	0.00	0.14	0.14
u_d			0.104			0.039
t			1.618			0.301
$p<$			0.955			0.577

affected mussel species nonselectively and that postdrought abundance of a species was mostly a function of the predrought abundance of that species.

Even though the species in our small-stream study sites declined at similar rates, the drought resulted in a drainagewide shift toward a more homogenized fauna. Over all sites, predrought and postdrought site assemblages were distinctive and the postdrought fauna showed higher within-group similarity than the predrought samples. The within-year homogeneity of the fauna was significantly greater than expected by chance (MRPP: $t = -20.05$, $P < 0.000001$), and the average within-group distance decreased from 1.61 in 1993 to 0.448 in 2002. The results of a principal components analysis corroborate and illustrate this shift (Figure 3). The first two principal component axes accounted for only 22.3% of the total variance, but the vectors between all site–year centroid pairs showed postdrought shifts toward the center of the species abundance space, indicating convergence on a shrinking species pool. The shifts are most pronounced in Sipsey Fork and Flannagin Creek and were influenced by a loss or decrease of large-stream species (Sipsey Fork) and of *Villosa* spp. and *Pleurobema furvum* (Flannagin Creek).

Discussion

Drought Effects among Streams

Streams differed widely in the extent to which their mussel faunas were affected by severe drought. Larger streams that maintained substantial flow, including regulated and unregulated streams, were affected little by drought. Even though isolated instances of high mussel mortality occurred in dewatered areas along the stream margins, overall unionid abundance and assemblage composition did not change detectably at any large-stream site. In contrast, the drought devastated small-stream mussel faunas.

Because it was dewatered almost completely, Flannagin Creek experienced the greatest direct loss of habitat due to the drought. As expected, overall mussel abundance and species richness declined dramatically in the stream. The absence of live mussels after the drought in sections of the streambed that had been dewatered shows that mussels were unable to withstand emersion by burying in the substrate. Mussels that did survive the drought did so only in the few sections of the channel that remained wetted.

Surprisingly, the other four small study streams experienced declines in overall mussel abundance

TABLE 5.—Changes in mussel abundance (number/m^2) by species at five sites in Bankhead National Forest before and after the drought of 2000. Species that were found at a site but not encountered in quantitative sampling are denoted by having abundance values less than those of species that were represented in quantitative sampling by only one individual. The test statistic t is for a one-tailed randomized paired t-test; $P < 0.05$*, $P < 0.01$**; NA = not applicable.

Stream	Species and statistic	Predrought	Postdrought	Difference
Brown Creek	*Hamiota perovalis*	0.96	0.21	−0.76
	Medionidus acutissimus	0.28	0.03	−0.25
	Strophitus subvexus	0.28	0.03	−0.25
	Villosa lienosa	0.08	0.06	−0.21
	V. vibex	0.04	0.03	−0.01
	Mean			−0.26
	t			−1.907*
Brushy Creek	*Hamiota perovalis*	0.62	0.12	−0.49
	Medionidus acutissimus	0.27	0.05	−0.22
	Strophitus subvexus	0.12	0.03	−0.09
	Villosa lienosa	0.04	0.03	−0.01
	V. nebulosa	<0.04	0	NA
	V. vibex	0.12	0.03	−0.09
	Mean			−0.18
	t			−2.108*
Flannagin Creek	*Hamiota perovalis*	0.55	0.11	−0.44
	Lampsilis straminea	<0.04	0	NA
	Medionidus acutissimus	0.16	0	−0.16
	Pleurobema furvum	0.12	0	−0.12
	V. lienosa	1.22	0.17	−1.05
	V. nebulosa	2.24	0.38	−1.86
	V. vibex	0.04	0.06	0.02
	Mean			−0.60
	t			−1.969*
Rush Creek	*Hamiota perovalis*	0.80	0.24	−0.56
	Lampsilis straminea	0.08	0.03	−0.05
	Medionidus acutissimus	0.08	0.03	−0.05
	Pleurobema furvum	0.08	0	−0.08
	Strophitus subvexus	0.56	0.15	−0.41
	V. lienosa	0.08	0.09	0.01
	V. nebulosa	0.08	0.03	−0.05
	V. vibex	0.16	0.12	−0.04
	Mean			−0.16
	t			−2.142**
Sipsey Fork	*Elliptio arca*	0.16	<0.02	−0.14
	E. arctata	<0.04	0.02	NA
	Hamiota perovalis	0.28	0.09	−0.19
	Lampsilis ornata	0.04	<0.02	−0.04
	L. straminea	<0.04	0	NA
	Pleurobema furvum	0.48	0.18	−0.30
	Potamilus purpuratus	WD	0	NA
	Ptychobranchus greeni	0.88	0.18	−0.70
	Quadrula asperata	0.04	0.05	0.01
	Q. verrucosa	0.28	0.07	−0.21
	Strophitus subvexus	0.04	0.02	−0.02
	Toxolasma corvunculus	0	0.02	0.02
	Villosa lienosa	0	0.02	0.02
	V. nebulosa	<0.04	0.23	0.21
	V. vibex	<0.04	0	NA
	Mean			−0.12
	t			−2.031*

similar in magnitude to the decline in Flannagin Creek, even though these streams remained mostly watered throughout the drought. From this, we conclude that stream-dwelling mussel species are highly susceptible to secondary effects of drought in addition to direct drying of stream habitat. Similar to our study, small streams in the Flint River drainage, Georgia, that stopped flowing in the 2000 drought but retained water in the channel experienced declines in mussel abundance; however, mussels did not decline in other streams that maintained flow (Golladay et al. 2004). In nonflowing streams, dissolved oxygen declined with decreases in flow and higher mortality occurred among several mussel species at dissolved oxygen levels less than 5 mg/L (Johnson 2001). In streams with abundant populations of *Corbicula fluminea*, Asian clams died before native mussels, accelerating declines in dissolved oxygen due to decomposition (Johnson 2001).

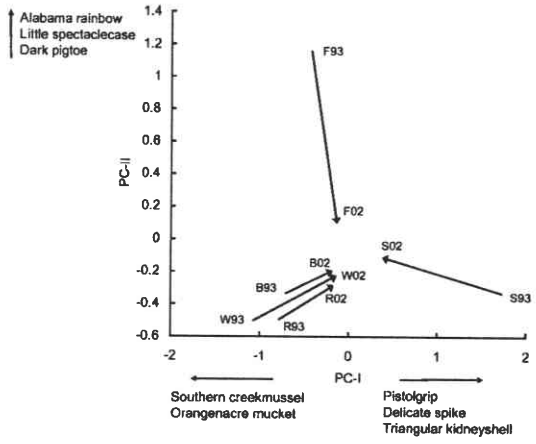

FIGURE 3.—Principal components (PC) axes and mean scores of small-stream sites in Bankhead National Forest, Alabama, ordinated by mussel species abundances. Species listed on axes are those that loaded heavily on each axis. The vectors indicate the direction and magnitude of change in the centroid of mussel assemblages at each site between the predrought (1993) and postdrought (2002) surveys. Abbreviations for streams are as follows: B = Brushy Creek, F = Flannagin Creek, S = Sipsey Fork, R = Rush Creek, and W = Brown Creek.

In our small-stream sites, abundance of *C. fluminea* declined precipitously in Sipsey Fork, which remained watered but experienced near-zero flows, and at Flannagin Creek, which dried extensively but retained a few isolated pools. We hypothesize that heavy accumulations of fallen leaves, lack of flow, and above-normal water temperatures (U.S. Geological Survey, 02450250; waterdata.usgs.gov/al/nwis) combined to produce severely and abnormally low levels of dissolved oxygen in our small study streams. As a likely result of the low dissolved oxygen levels, *C. fluminea* experienced near total mortality, and unionids experienced high mortality, even in streams that retained water throughout the drought.

Effects of the Drought on Mussel Assemblages

Overall mussel abundance did not decline during the drought at any large-stream site, but the abundance of a few species did appear to decline. However, all estimated declines of individual unionid species were low and often variable among sites, and abundance of other species showed modest increases during the same period. These results were probably caused by normal population fluctuations and sampling error and are not necessarily related to drought. Similarly, the large increase in *Corbicula fluminea* abundance at the Little Tallahatchie River and Sipsey River site 2, along with unchanged *C. fluminea* abundance at Sipsey River site 1, probably reflects the high degree of population variability inherent in this short-lived, highly fecund species (Stites et al. 1995) and is in direct contrast to the response of the species in our small-stream sites.

We have strong evidence that the drought affected all species similarly in small streams. We roughly doubled the area sampled postdrought to increase our power to detect changes in mussel assemblages. Estimates of assemblage richness are dependent primarily on the number of individuals encountered rather than the area sampled (Gotelli and Graves 1996). Even though we sampled less area predrought, we encountered from 1.5–3.5 times as many individuals predrought as postdrought except in Rush Creek, where we encountered similar numbers of individuals. If sample bias is present, we would expect true postdrought species richness to be slightly higher than we estimated because we collected a smaller number of mussels postdrought; however, the presence of such bias would only strengthen our conclusion that there were few observable changes in richness. In reality, bias of this type is low in our samples despite differences between years in the number of individuals encountered. At most sites, we found the same species both predrought and postdrought. The only site that had noticeably lower richness postdrought was Flannagin Creek, a stream that dried almost completely during the drought. Furthermore, with the exception of a single specimen of *Toxolasma corvunvulus*, postdrought sampling found the exact same species forest-wide as in larger-scale surveys conducted predrought (McGregor 1992; Haag and Warren 1998). These observations, together with consistent rates of declines across all species and strong correlations between mean abundance of species predrought and postdrought indicate that the likelihood of surviving the drought was mostly a function of predrought abundance and not due to relative differences in drought tolerance among species.

The only unionid population that showed convincing evidence of an increase during our study was *Villosa nebulosa* in Sipsey Fork, which was rare before the drought but represented the most abundant species postdrought. In our study streams, this species occurs commonly in pools and riffles; therefore, at this site, the largest among our small-stream sites, *V. nebulosa* may have fared better than species that occur typically in shallower habitats. In smaller streams with few deep pool refugia (e.g., Flannagin Creek), *V. nebulosa* declined greatly, similar to other species.

In contrast to our finding that species were affected similarly by drought, species in the Flint River basin varied in their tolerance to drought stress. Species of *Lampsilis*, *Medionidus*, and *Pleurobema* showed

increased mortality at dissolved oxygen levels below 5 mg/L, but other species, including *Villosa lienosa* (little spectaclecase) and *V. vibex* (southern rainbow), were affected little by low dissolved oxygen and survived extended periods of emersion (Johnson 2001). In Bankhead National Forest, *V. lienosa, V. nebulosa,* and *V. vibex* were among the few species that had estimated declines less than 50%, but in most cases, their low predrought abundance precluded making precise estimates of decline. At Flannagin Creek, the only site where species of *Villosa* were abundant in predrought samples, *V. lienosa* and *V. nebulosa* both had estimated declines exceeding 80%, indicating that even species with potentially greater drought tolerance suffered high mortality. In a laboratory study, mussel species from lentic or depositional habitats were able to regulate oxygen consumption at low dissolved oxygen levels better than species inhabiting lotic habitats, but species from both habitat types performed worse at higher temperatures (Chen et al. 2001). The mussel fauna of Bankhead National Forest is predominated by lotic species, which are probably not well adapted to low oxygen conditions. Furthermore, the severity of the 2000 drought, including extended periods of high temperatures, probably transcended interspecific differences in drought tolerance that could be manifested as differential survival under less severe stress.

Even though most species were affected similarly and basinwide species richness was unchanged after the drought, we detected subtle changes in assemblage composition that portend a long-term erosion of mussel diversity in Bankhead National Forest. Changes in assemblage composition were due primarily to the loss of rare species and declines in locally abundant populations of species that were otherwise rare over most of the forest (e.g., *Villosa nebulosa* and *V. lienosa*) and previously gave distinctiveness to these local assemblages. The resultant postdrought fauna was characterized by a shift toward drainagewide homogenization with convergence on a shrinking species pool.

Long-Term Effects in the Bankhead National Forest

The steep decline in mussel abundance that we observed in small streams in Bankhead National Forest between 1993 and 2001–2002 is attributable to the drought of 2000. The protection afforded these watersheds by the Endangered Species Act, federal ownership, and wilderness status excludes them from many threats faced by streams in landscapes with heterogeneous ownership (Brim-Box and Mossa 1999; Arbuckle and Downing 2002). Although a number of activities could have impacted mussel populations (e.g., timber harvest, road construction, and horseback riding), it is unlikely that such activities would have caused the dramatic declines that we observed over the entire forest. Further, introduced *Corbicula fluminea* showed much greater declines than unionids during that period. *C. fluminea* is more tolerant than unionids of a wider range of stream perturbations, with the exception that *C. fluminea* is more sensitive to the low dissolved oxygen levels typically associated with drought than are many unionid species (McMahon 2001; Golladay et al. 2004). Although we have no quantitative data on mussel abundance in the years immediately before the drought, we visited most of the study streams on numerous occasions between 1994 and 1999 (e.g., Haag and Warren 1997; Haag and Warren 2000). During these visits, mussels remained common and easy to find, suggesting that the decline occurred rapidly, sometime after 1999. Finally, the postdrought occurrence of mussels only in sections of Flannagin Creek that retained water during the drought convincingly identifies drought as the cause of observed declines in mussel abundance.

An encouraging note for the future of the mussel fauna in the forest is that all of the species present before the drought were also found alive postdrought. In addition, *Toxolasma corvunculus* was not previously known from Bankhead National Forest; our collection in 2002 represents an addition to the known fauna of the forest and represents one of the few times this critically imperiled species has been found alive anywhere in the last 25 years (J. D. Williams, U.S. Geological Survey, personal communication; NatureServe 2006). Despite the severe depression of mussel abundance after the drought, the species pool exists for a hypothetical full recovery of the fauna.

In reality, the small postdrought population sizes of most species, coupled with the low reproductive rate of freshwater mussels (Haag 2002), probably will make recovery of this fauna a slow process, the outcome of which will be variable among species. Populations of species that penetrate headwaters and occupy many kilometers of contiguous habitat within the forest (e.g., *Hamiota perovalis* [orange-nacre mucket], *Medionidus acutissimus* [Alabama moccasinshell], *Strophitus subvexus* [southern creekmussel], and *Villosa* spp.) may eventually recover fully from the 2000 drought and be viable into the foreseeable future. In contrast, small, isolated populations of headwater species (e.g., above Brushy Lake) and small populations of large-stream mussel species may not recover easily from severe reductions in population size caused by the drought.

Mussel species characteristic of large streams, such as *Elliptio* spp., *Lampsilis ornata* (southern pocketbook), *Potamilus purpuratus*, *Ptychobranchus greeni* (triangular kidneyshell), *Quadrula asperata* (Alabama

orb), and *Q. verrucosa* (pistolgrip), are at particularly high risk of local extinction in Bankhead National Forest. Each of these species is represented in the forest only by small populations restricted to the lower reaches of Sipsey Fork and Brushy Creek. These populations are isolated from each other by Lewis Smith Reservoir, as well as from other populations in the Mobile Basin. Changes in mussel assemblage composition in response to the drought were driven in part by decreases in abundance of large-stream species. If postdrought population sizes are below the minimum necessary for successful reproduction, these populations may be in a downward spiral of abundance from which they will have difficulty recovering. Because the populations cannot receive immigrants, any potential rescue effect is precluded. Based on the collection of a single, weathered shell of *Potamilus purpuratus* in Sipsey Fork in 1993, but the absence of live individuals in 1993 or 2002, this large-stream species is apparently now extirpated from the forest. Although common elsewhere in the Mobile Basin, its loss was probably due to small initial population size and isolation; these factors threaten large-stream and other rare species in the forest and will probably result in continued erosion of mussel diversity over time.

Conclusions

Our results, along with the few other published studies on mussel response to drought, show that the ability of freshwater mussels to withstand severe drought is highly dependent on the stream context in which they occur. Owing to their limited mobility and inability to withstand long periods of emersion, stream-dwelling mussels experience high mortality as a result of drying of their habitat. However, mussels are also highly susceptible to secondary effects of drought associated with cessation of flow. Secondary effects of drought appear related primarily to low dissolved oxygen levels (Johnson 2001; Golladay et al. 2004). In our study, streams that remained flowing during the drought showed no declines in mussel numbers, but streams that stopped flowing experienced severe reductions in mussel abundance regardless of the extent to which the streambed was dewatered. In addition to drought, similar negative effects on mussel faunas can be expected in regulated streams that periodically experience drastically reduced flows in combination with high temperatures and increased biological oxygen demand, even when reduced flows do not result in exposure of the streambed.

Drought is probably one of the major stressors limiting headwater mussel faunas and may preclude the accumulation of the high-density mussel beds characteristic of larger streams. Historically, mussel populations in small streams that were reduced or eliminated by periodic drought probably rebounded relatively quickly because of immigration from downstream populations that were less affected by drought. In today's highly fragmented landscape, drought represents one of the major natural threats to the long-term viability of isolated remnant headwater mussel communities. Despite the large size of Bankhead National Forest, many resident mussel populations are now at critically low levels owing to the drought of 2000 and may not be viable without expensive and ecologically risky conservation measures such as supplemental stocking of hatchery-raised individuals. The current status of the Bankhead National Forest mussel fauna provides a clear example of the difficulties inherent to conservation in isolated conservation refuges.

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