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[Article]

Recolonization by Warmwater Fishes and Crayfishes after Severe Drought in Upper Coastal Plain Hill Streams

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Abstract.—Extreme hydrologic disturbance, such as a supraseasonal drought, can dramatically influence aquatic communities. Documentation of the responses of aquatic communities after such disturbances provides insight into the timing, order, and mechanisms of recolonization. Postdisturbance recolonization of streams depends on many factors, including the region and characteristics of the disturbance relative to the disturbance regime. A supraseasonal drought that ended in the fall of 2000 resulted in the desiccation of numerous small streams or stream segments in northern Mississippi that were normally perennial. We repeatedly sampled fish and crayfish during predrought and postdrought periods in seven stream reaches that dried and five that remained flowing during the drought. From immediately after the drought until early summer of 2001, postdrought fish and crayfish assemblages differed from predrought assemblages in dry sites but not in flowing sites. The initially slow recolonization rates increased considerably during early spring 2001 so that by June 2001 fish catch per unit effort, species composition, and species richness in dry sites no longer differed significantly from predrought values. The fish recolonization process was highly ordered, as indicated by significant patterns of species nestedness over time in dry sites. Crayfish numerical recovery followed a pattern similar to that for fish, and we captured more crayfish in June 2001 than in the predrought period. Patterns in fish and crayfish population size structures over time indicated that repopulation was due to both immigration and reproduction. Recolonization was indicative of high mobility, particularly during spring and early summer. Although the fauna was quite resilient to stream desiccation, the effects on fish species composition and fish and crayfish size structure persisted 1 year after the drought.

Disturbance, often in the form of floods or droughts, can be influential in structuring lotic communities. The extent of the influence depends in part on the nature, severity, and return intervals of disturbances (Meffe and Minckley 1987; Resh et al. 1988; Poff and Allan 1995; Dodds et al. 2004). Extreme, or supraseasonal, drought (Lake 2003) can completely desiccate perennial stream segments, temporarily eliminating entire fish assemblages from affected segments (Bayley and Osborne 1993). Because supraseasonal drought is not a predictable disturbance to which animals must respond regularly, patterns of recovery after supraseasonal droughts can differ dramatically from those occurring after seasonal or periodic droughts (Lake 2003). Nonetheless, resistance and resilience to supraseasonal drought are expected to differ among regions based on different degrees of adaptation to seasonal drought (Poff and Ward 1990; Dodds et al. 2004).

The rates and mechanisms of stream recolonization after drought depend on many factors, including the species pool (Larimore et al. 1959; Lonzarich et al. 1998), presence of refugia (Sedell et al. 1990; Meador and Matthews 1992; Taylor and Warren 2001; Magoulick and Kobza 2003), size and distribution of source populations (Sheldon and Meffe 1995; Lonzarich et al. 1998), and recruitment (Larimore et al. 1959; Bayley and Osborne 1993). Typically, species richness recovers before fish abundance (Detenbeck et al. 1992; Sheldon and Meffe 1995; Lonzarich et al. 1998). The timing and spatial scale of the disturbance strongly influence short-term (e.g., <5 years) recovery (Detenbeck et al. 1992). For example, the seasonal timing of disturbance relative to fish spawning periods influenced postdisturbance recovery of fish densities by 6 months or more (Niemi et al. 1990; Detenbeck et al. 1992).

Far less is known about crayfish resistance and resilience to drought (Dodds et al. 2004), and no published work addresses disturbance responses by the species common in this study. Interspecific variation in crayfish response to drought appears to be partly attributable to differences in resistance arising from varying burrowing habits (Taylor 1983, 1988). Some species are well adapted to routine stream desiccation, but differences in tol-

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TABLE 1.—Locations of sample sites (D = sites that were dry during drought, F = flowing sites) in Benton and Lafayette counties, Mississippi (for more location detail, see Warren et al. 2002). Stream and reach sizes, including low-flow wetted width and streamflow (represented by June 2001 values), predrought (pre) and postdrought (post) reach lengths, postdrought electrofishing effort, and hydrologic conditions (water status) during the drought (Oct 6–Nov 7 2000) are shown. Sampling dates are presented, and column headings indicate how groups of sample dates are referred to in the text.

Site	Creek	Coordinates	Watershed area (ha)	June 2001 Stream flow (m^3/s)	June 2001 Mean width (m)	Reach length Pre (m)	Reach length Post (m)
D1	Oaklimeter	34°39′59.0″N, 89°06′19.4″W	261	0.0000	1.5	80	160
D2	Tributary to Potts	34°36′13.2″N, 89°18′55.6″W	332	0.0008	1.1	80	160
D3	Tributary to Puskus	34°27′02.6″N, 89°21′00.2″W	272	0.0085	2.2	80	160
D4	Puskus	34°23′43.2″N, 89°22′20.7″W	441	0.0265	2.8	80	160
D5	Yellow Leaf	34°22′48.0″N, 89°24′38.0″W	221	0.0246	2.7	80	160
D6[c]	Kettle	34°17′58.8″N, 89°19′48.3″W	1,697	0.0192	3.1	80	160
D7	Kettle	34°20′41.8″N, 89°20′12.3″W	185	0.0006	0.9	80	160
F1	Yellow Rabbit	34°49′09.3″N, 89°06′19.0″W	886	0.0319	3.4	92	192
F2	Puskus	34°26′41.0″N, 89°20′14.8″W	4,672	0.1785	6.2	144	216
F3	Puskus	34°23′43.7″N, 89°22′18.3″W	925	0.0516	4.4	96	160
F4	Yellow Leaf	34°22′27.0″N, 89°25′17.0″W	859	0.0671	3.8	80	160
F5	Kettle	34°20′07.1″N, 89°19′53.5″W	591	0.0065	1.6	80	160

[a] <100 m downstream of reservoir. One large pool persisted below the reservoir outflow upstream of the study reach, but none persisted in the study reach.

[b] Persistence of some flow was possible.

[c] The predrought site was 1.4 km upstream, 10 m upstream of Mississippi Highway 6 at 34°18′48.6″N, 89°19′42.1″W.

erance to periodic stream drying are evident even within genera (Flinders and Magoulick 2003).

A supraseasonal drought in northern Mississippi resulted in the cessation of all surface water flow in numerous small, normally perennial streams, and stream segments became completely dry or were reduced to a few stagnant, isolated pools during the summer and fall of 2000. To understand how stream drying influenced stream communities, we examined the extent, seasonal timing, and mechanisms of fish and crayfish assemblage recovery for 1 year after surface flows resumed. Our primary objectives were to (1) determine the rates and seasonality of fish recolonization after drought by comparing assemblage characteristics before stream desiccation and periodically after flows resumed; (2) determine mechanisms of fish recovery (e.g., immigration, reproduction) by following changes in population size structure over time; (3) quantify species-specific immigration probabilities and extent of numerical recovery to identify fish species that were particularly rapid or slow recolonizers; and (4) determine the extent, seasonality, and mechanisms of recovery in crayfish densities.

Study Area and Drought Characterization

We selected 12 stream sites (Table 1) in upper Coastal Plain hills of the Little Tallahatchie River drainage (upper Yazoo River basin), Mississippi, that we had sampled in summer 1999 before the drought (Figure 1). Most streams in the study area are deeply incised, and the typically unstable substrate is predominantly sand or silty sand; occasional gravel or hard clay is present in some sites.

We quantified the drought by means of drought indices and local rainfall records. The standardized precipitation index (Hayes 2003) calculated over 6- and 12-month periods preceding November 2000 revealed that north-central Mississippi was "extremely dry" (driest category; index ≤ −2; return interval less than 1 in 50 years; NDMC 2001a). The Drought Monitor, a synthesis of six key drought indices plus supplemental indicators (NDMC 2004), revealed that drought developed in the study area from October 1999 through July 2000, intensified and became "exceptional" (return interval < 1 in 50 years) by October 2000, and persisted as at least a moderate drought in part of the study area through early February 2001 (NDMC 2001b). Rainfall at four local weather stations (Figure 1) from November 1999 through October 2000 averaged 59% of the 30-year normal (NOAA 1999, 2000a); rainfall deficits increased during the summer of 2000 (Figure 2). Above-normal rain fell during November 2000, including 6–13 cm on November 8 and 9 (NOAA 2000b).

Continuous surface flow resumed between late October and December 2000 at all sites; exact dates are unknown for most sites. Several sites

TABLE 1.—Extended.

			Sample dates					
				Postdrought				
Site	Post mean electrofish time (s) (SD)	Water status	Predrought 1999	Nov 2000	Jan 2001	Apr 2001	Jun 2001	Nov 2001
D1	785 (20.1)	1 pool[a]	29 Jun	5 Dec	31 Jan	9 Apr	20 Jun	5 Nov
D2	799 (4.0)	Dry	22 Jun	5 Dec	31 Jan	9 Apr	20 Jun	5 Nov
D3	807 (13.6)	Pools	28 Jul	14 Nov	30 Jan	10 Apr	22 Jun	8 Nov
D4	803 (4.1)	Dry	2 Jun	4 Dec	30 Jan	10 Apr	18 Jun	8 Nov
D5	802 (2.7)	Dry?[b]	9 Jun	14 Nov	1 Feb	11 Apr	19 Jun	7 Nov
D6[c]	810 (13.2)	Dry	8 Jun	13 Nov	1 Feb	11 Apr	21 Jun	6 Nov
D7	730 (158.5)	1 pool[a]	10 Jun	5 Dec	30 Jan	11 Apr	21 Jun	6 Nov
F1	950 (26.5)	Flowing	21 Jul	7 Dec			20 Jun	9 Nov
F2	1,092 (17.0)	Flowing	3 Aug	15 Nov			22 Jun	
F3	813 (11.9)	Flowing	2 Jun	4 Dec			18 Jun	8 Nov
F4	922 (105.6)	Flowing	9 Jun	14 Nov			19 Jun	7 Nov
F5	810 (10.5)	Flowing	10 Jun	13 Nov			21 Jun	6 Nov

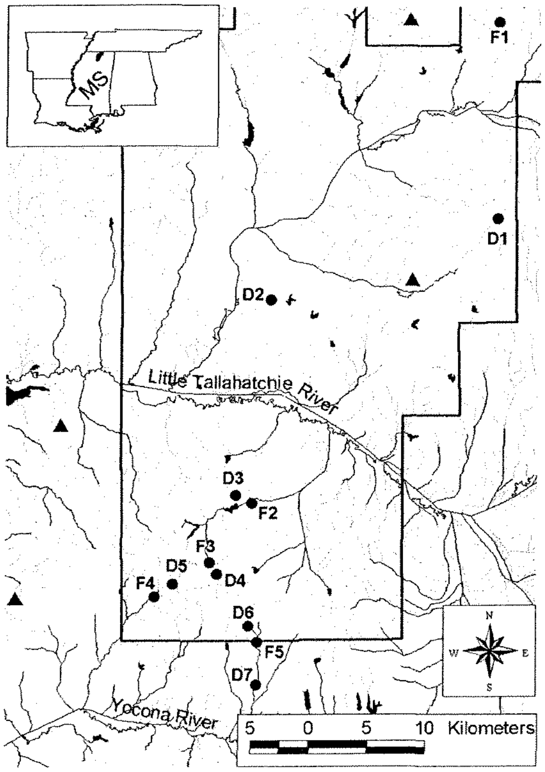

FIGURE 1.—Locations of study sites (circles) and weather stations (triangles) in northern Mississippi (study area location in inset). Letters in site codes indicate sites that were dry (**D**) versus flowing (**F**) during the drought in 1999–2001. The bold line delineates the border of the Holly Springs National Forest. See Table 1 for a description of each study site.

flowed intermittently in the fall before continual flows were re-established. In sites receiving unregulated discharge from small reservoirs (sites D1 and D7), flow continued longer into the drought but resumed later than in sites not influenced by reservoirs.

Methods

We quantitatively sampled fish, crayfish, and stream habitat at seven sites where surface flows ceased during the drought and at five sites where flows continued throughout the drought. To distinguish between sites that ceased flowing and those that did not, we refer to the former as "dry" sites (even though several had persistent, isolated pools in or near the sample reaches; Table 1) and to the latter as "flowing" sites. Although dry sites were nearly or completely dry during the drought, they were flowing during our standardized sampling (see below for exceptions). We used data from flowing sites as references for patterns observed in dry sites but not to quantify drought effects in the flowing sites per se. "Predrought" refers to samples collected in summer 1999 before the drought, whereas "postdrought" refers to all samples collected after streamflows resumed (Table 1).

We initiated postdrought sampling on November 13–15 and December 4–7, 2000, soon after surface flows resumed in each dry site; we sampled each flowing reference site during the same week as the nearest dry site. During 2001, we sampled dry sites four more times and flowing sites two more times

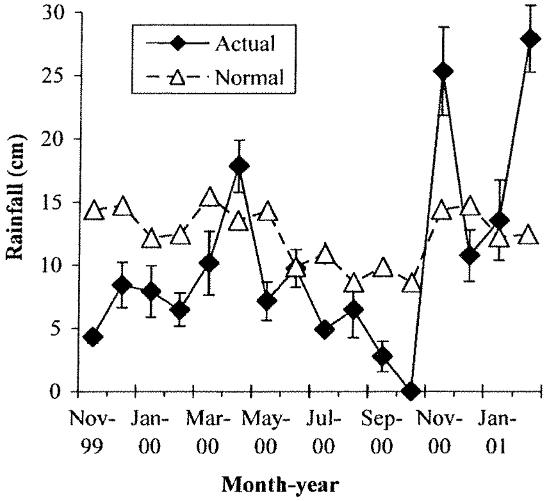

FIGURE 2.—Monthly actual and normal (30-year average) rainfall amounts from November 1999 to February 2001, averaged (±SD) across four weather stations (see Figure 1) located near the northern Mississippi study area (NOAA 1999, 2000a, 2000b, 2001). Many of the SD bars are smaller than the symbols.

(except site F2; Table 1). Inclement weather prevented us from sampling site F2 in November 2001. After the drought, we moved site D6 1.4 km downstream of the predrought location, which was impounded by a beaver dam.

Field methods.—At dry sites (except D5), we walked upstream and downstream until we reached flowing water, a reservoir, or 1 km in distance. We did not examine dry site D5 during the drought, but we found that a stream segment 0.8 km downstream of D5 was completely desiccated. We documented any isolated pools within the stream segment and used dip nets or seines to sample fish and crayfish in isolated pools. We could only sample the margins of the large, deep plunge pool below each reservoir. These pools may have provided refugia for species not encountered in other isolated pools.

We delineated sample reaches based on average wetted stream widths during our 1999 sampling. In 1999, we sampled reaches that were 20 times the average wetted stream width (minimum, 80 m; Table 1) (Warren et al. 2002) and subdivided each reach into four equal subreaches. During the postdrought period, we sampled the same subreaches that were sampled in 1999 prior to the drought but added four additional subreaches at each site (except site F2, which had six postdrought subreaches; Table 1); thus, postdrought reaches were twice as long as predrought reaches. Except in the largest stream (F2), postdrought reach lengths were 40 or more times the low-flow stream width (minimum, 160 m; maximum, 216 m).

In each subreach, we sampled for fish and crayfish in an upstream direction. We used single-pass backpack electrofishing (Smith-Root model 12A programmable output wave, battery-powered electrofisher set at 60 Hz, 6-ms pulse width, and 400–500 V) without block nets, and then sampled by seining (3 m wide × 2 m deep; 3.2-mm mesh). Sampling effort in each subreach was consistent over time. We electrofished for about 5 s per meter of subreach length (Table 1). Depending on stream size, one to three people dipnetted fish, the number remaining constant at each site over time. We made two seine hauls per subreach (16 per site) except at site F2 (three hauls per subreach; 18 total). One haul consisted of a sustained drag of the seine, usually in pools or runs, or one set-and-kick in riffles (Jenkins and Burkhead 1994) and areas with abundant wood where we could not drag the seine. Seining methods (i.e., drags and set-and-kicks) and effort were consistent within subreaches over time.

In predrought sampling, we preserved most fish and crayfish for laboratory identification. We measured body lengths of crayfish, and C.A. Taylor (Illinois Natural History Survey) identified all crayfish specimens. In postdrought sampling, we kept animals in live buckets on site, processed them in the field (species identification and total length [TL] class), and then released them in the subreach of capture. The few fish we could not identify in the field (mostly age 0) were preserved for laboratory identification. We counted all crayfish captured in postdrought sampling and returned most to the streams. We were unable to identify crayfish to species in the field, but we preserved several individuals of each ostensible species encountered for later identification. Beginning in April 2001, we assigned crayfishes to size-classes (body length) of less than 2.5 cm, 2.5–5.0 cm, and greater than 5.0 cm.

After sampling biota, we characterized physical habitat. We measured wetted stream width at three equidistant locations in each subreach (18–24 widths per reach) and counted pieces of large wood in each subreach. We visually determined the dominant substrate every 3 m throughout each reach. Because dominant substrate and the number of large wood pieces varied little throughout the study, they were excluded from analyses. We calculated stream discharge from depth and velocity measurements taken along one transect per reach during each sample (Harrelson et al. 1994). In sites with isolated pools during the postdrought period, we measured the wetted stream lengths in each subreach. Basic habitat parameters were characterized by comparable methods in predrought sampling (Warren et al. 2002). We determined watershed areas from geographical information systems coverages.

Data Analyses

Fish.—We conducted a variety of analyses to assess the "recovery" of fish assemblage structure (species composition and relative abundance) and to explore the patterns and mechanisms of recovery (see Appendix 1 for a list of fish species). In some analyses, we compared predrought and postdrought data only within dry sites; in others, we also compared data or patterns between dry sites and flowing reference sites. We report quantitative results as catch per unit effort (CPUE; fish/min of electrofishing), which we view as an index of abundance. We combined electrofishing and seine data *only* for analyses based solely on species presence–absence (i.e., species richness, assemblage nestedness, and immigration probability) but not for those that included an index of abundance (e.g., assemblage similarity). By combining species from the two sampling methods, we gained better approximations of site species richness by increasing the probability of detecting a species on any given sampling date. We used randomization routines (Blank et al. 2001) to determine *P*-values for the *t*-tests, analyses of variance (ANOVAs), and correlations described below (10,000 iterations, $\alpha = 0.05$ for all tests; Manly 1997).

Assemblage similarity.—To inferentially test hypotheses of no fish assemblage differences between pre- and postdrought samples, we used a blocked multiresponse permutation procedure (MRPP) with Euclidian distance (PC-Ord 4.01; McCune and Mefford 1999; McCune and Grace 2002). The MRPP is a nonparametric randomization analog of parametric procedures like discriminant analysis but has the advantage of not requiring distributional assumptions (Mielke and Berry 2001). The blocked MRPP test statistic T indicates the amount of separation between groups (sampling periods), and the chance-corrected within-group agreement statistic A indicates effect size. We used sites as blocks so that samples from a given site were paired, and we did not use median alignment. Testing dry and flowing sites separately, we compared assemblages among all dates as well as between the predrought sample and each postdrought sample. To balance the design for flowing sites, we excluded site F2, which was sampled only twice after the drought.

Species richness.—We defined species richness as the total number of fish species collected by electrofishing and seining. Because our sampling effort at each visit was doubled after the drought, our sampling design was biased toward finding more species during the postdrought period than during the predrought period.

We used paired, one-sided *t*-tests to compare pre- with postdrought species richness within sites. We compared predrought species richness to the species richness observed for each postdrought sample period, assessing dry and flowing sites separately.

We also tested for differences in species richness between dry and flowing sites. Using ANOVA, we first tested for overall differences in species richness among all sample groups from the four sample periods when both dry and flowing sites were sampled. After finding that the overall ANOVA was significant, we conducted ANOVA on species richness in dry versus flowing sites for each sample period.

Catch per unit effort.—Using electrofishing data only, we compared pre- with postdrought fish CPUE (all species combined) within sites. We used paired, one-sided *t*-tests to compare the predrought CPUE to the CPUE calculated for each postdrought sample; dry and flowing sites were tested separately.

We also compared CPUE between dry and flowing sites. We used ANOVA to test for overall differences in all sample groups from sample periods in which we sampled both dry and flowing sites. After detecting significant overall differences, we used ANOVA to test for differences in CPUE between dry and flowing sites from each sample period.

Recolonization patterns.—To examine the degree of nestedness of fish assemblages over time, we calculated the temperature (T°) of the sample × species presence–absence matrix for each dry site (Atmar and Patterson 1993; Taylor and Warren 2001). If species accumulated over time incrementally and persisted once they recolonized, we would expect a high degree of nestedness (low T°). We used a permutation approach (5,000 randomizations) to determine the probability of obtaining the observed distribution of species over time by chance (Atmar and Patterson 1995; Taylor and Warren 2001). Matrix temperatures characteristically increase as matrix rank increases, as percent fill approaches 50%, and as the matrix becomes more square (Atmar and Patterson 1995). Therefore, to assess normalized effect size among sites, we also used the number of standard deviation units (σ) by which each observed T° diverged from the mean of its randomly generated populations.

Immigration probabilities.—Calculating species' immigration probabilities allowed us to test for correlations in immigration among species and studies and to explore associations between immigration and other assemblage and site variables. We analyzed only data from dry sites, limited the analysis to the realized species pool for each site, and assumed that all species were absent during the no-flow period. We calculated an immigration probability for each species–dry site combination as the number of times a site was unoccupied at time t but occupied at time $t + 1$, divided by the number of times the site was unoccupied at time t (Taylor and Warren 2001). We calculated the site-specific immigration probability as the mean across species at a site and calculated the species-specific immigration probability as the mean across sites for a species. For each species, we also calculated mean pre- and postdrought CPUE (the latter averaged across all postdrought sample dates). Using only species that occurred at more than one site during predrought sampling, we tested for correlations between mean species-specific immigration probability and the mean predrought CPUE, mean postdrought CPUE, and number of sites occupied by the species during the predrought period. Similarly, we tested for correlations between mean site-specific immigration probability and other site characteristics: watershed area, total site species richness, and mean fish CPUE (averaged across all sample dates). For 14 species, we tested for a correlation between the mean species-specific immigration probabilities in our study and in an Arkansas study (Taylor and Warren 2001). Immigration probabilities were arcsine square-root transformed, and CPUE data were square-root transformed. Correlations were tested by use of a permutation correlation procedure with Pearson's coefficient.

Mode of fish recolonization.—We explored the importance of immigration versus reproduction in fish assemblage reestablishment by examining postdrought changes in CPUE over time for small fish ($\leq$4 cm TL [predominantly age 0]) and large fish (>4 cm TL [predominantly age 1 and older but including many age-0 fish in fall samples) in dry and flowing sites. We used paired t-tests to determine whether the mean CPUE for each size-class differed between the first and later postdrought sample periods.

Crayfish.—Although we ultimately generated a list of crayfish species occurring at each site (Appendix 2), we limited analyses to total numbers (all species combined) because we could not reliably identify species in the field. Crayfish from some genera and samples could not be identified to species even in the laboratory, because we did not encounter males in reproductive form. We excluded site F2 from crayfish data analyses because we sampled the site only three times and crayfish densities were always extremely low there; the maximum crayfish density (0.009 crayfish/m^2) at site F2 was an order of magnitude lower than that of any other site.

We used relative density, or the total number of crayfish captures (electrofishing and seining combined) standardized by reach area (number/m^2), as an index of change in crayfish numbers over time. Relative to the use of data from one method, the pooling of crayfish numbers from seining and electrofishing dramatically reduced sample variability and allowed us to detect consistent, interpretable temporal trends.

We tested for differences in pre- versus postdrought relative densities within sites. We conducted paired, two-sided t-tests of predrought crayfish density versus density in each postdrought sample. Separate analyses were performed for dry and flowing sites.

We also tested for differences in relative density between dry and flowing sites. First, using ANOVA, we tested for differences among all sample groups (for periods when we sampled both dry and flowing sites). After finding the overall ANOVA to be significant, we used ANOVA to compare relative densities in dry versus flowing sites for each sample period.

We compared predrought sizes of crayfish to postdrought sizes in June 2001 (the postdrought sample period most closely paired by dates with the predrought samples). We used paired, one-sided t-tests to determine whether the proportion of crayfish in the smallest size category was higher during the postdrought period than during the predrought period; we analyzed data from dry and flowing sites separately.

Results

Stream Habitat

Postdrought stream size variables differed between dry and flowing sites and over time. Al-

TABLE 2.—Results of blocked multiresponse permutation procedure tests of fish assemblages in dry and flowing sites in northern Mississippi streams for the following temporal comparisons: (1) among all samples, (2) between the predrought (1999) sample and each postdrought sample, and (3) between November 2000 and November 2001 samples. Data were catch per unit effort (fish/min) by species. Significant P-values (<0.05) indicate that assemblage differences among groups were greater than expected at random; T measures the separation of groups, and A measures the effect size.

Comparison	N	T	A	P-value
Dry sites				
All samples	42	−7.56	0.113	<0.001
1999 versus Nov 2000	14	−4.09	0.149	0.005
1999 versus Jan 2001	14	−4.33	0.171	0.005
1999 versus Apr 2001	14	−3.92	0.079	0.005
1999 versus Jun 2001	14	−1.53	0.014	0.069
1999 versus Nov 2001	14	−2.73	0.109	0.016
Nov 2000 versus Nov 2001	14	−3.43	0.109	0.010
Flowing sites				
All samples	16	−3.35	0.082	0.003
1999 versus Nov 2000	8	−1.76	0.063	0.055
1999 versus Jun 2001	8	−2.21	0.068	0.031
1999 versus Nov 2001	8	−1.15	0.032	0.126
Nov 2000 versus Nov 2001	8	−0.48	0.009	0.334

though overlap occurred, flowing sites were significantly larger than dry sites (Table 1) whether size was measured by wetted width, summer base streamflow during June 2001, or watershed area (Mann–Whitney $U_s = 4$; $N = 7, 5$; $P < 0.05$ for all measures). Initial postdrought discharge increased gradually in some dry streams and quickly in others. Discharge during sampling increased through the April 2001 sample and then decreased through the next fall, although storm peaks occurred between samples. The reservoir-influenced sites became intermittent again during the summer of 2001; this was apparently due in part to beaver-deposited debris partially obstructing reservoir outlet standpipes. In June and November 2001, site D1 was reduced to large, isolated pools that covered 84% of the reach length. At site D7, flow was extremely low in June 2001, and by November 2001 only the downstream 56% of the reach retained water.

Fish

Overall, we captured 6,943 fish representing 54 species from 14 families (Appendix 1). Cyprinidae, Centrarchidae, Percidae, and Fundulidae constituted 86% of fishes captured. We captured nearly 3,000 fish from dry sites and nearly 4,000 from flowing sites, and 75% of the captures were obtained during the postdrought period. We may have captured individual fish more than once during the postdrought period, however.

Assemblage Similarity

Assemblage similarity indicated recovery of dry-site fish assemblages by June 2001. Initially, postdrought fish assemblages in dry sites differed dramatically from predrought assemblages, but by June 2001 they were similar to predrought assemblages (blocked MRPP; Table 2). However, in November 2001, dry-site assemblages again differed significantly from predrought assemblages.

Conversely, fish assemblages in flowing sites were similar between the predrought period and the first postdrought sample in November 2000 (Table 2). Only the June 2001 assemblages differed significantly from the predrought assemblages in flowing sites.

Comparison of assemblages sampled immediately after the drought (November 2000) to those sampled 1 year later (November 2001) revealed a significant difference for dry sites but not for flowing sites (Table 2). The source of the difference between years in dry sites was the extremely low species richness and CPUE that were observed immediately after the drought.

Species Richness

Relative to predrought values, postdrought fish species richness in dry sites had recovered by the spring of 2001. Within dry sites, fish species richness was significantly lower during postdrought sampling than during the predrought period until April 2001 (paired, one-sided permutation t-tests: $t < -4.4$, $P < 0.01$ for significant tests; Figure

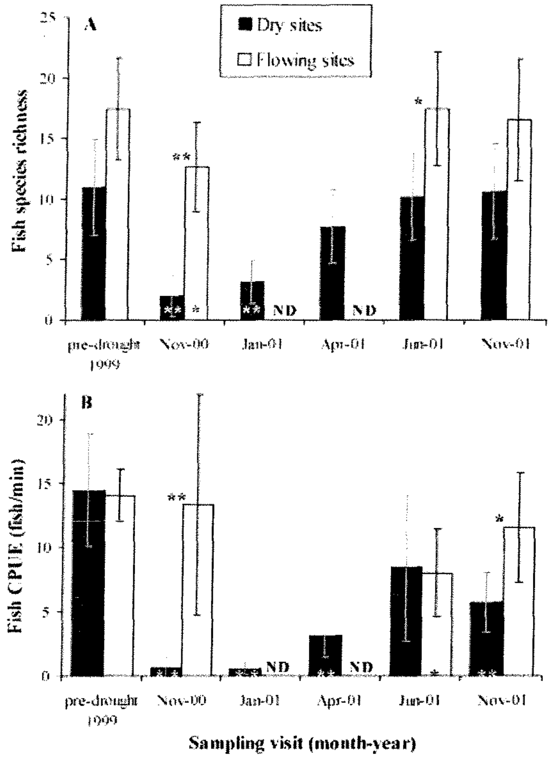

FIGURE 3.—Mean (±2 SEs) (**A**) species richness and (**B**) fish catch per unit effort (CPUE = fish caught/min of electrofishing) for each sample period in dry sites (during drought; see Methods) versus flowing sites in northern Mississippi. Predrought samples were collected in the summer of 1999; all other sampling occurred after the drought ended. Asterisks above bars indicate significant differences between dry and flowing sites (ANOVA). Asterisks at the bottom of a bar indicate significant differences between that sample group and the predrought group in the same category (paired, one-sided t-test: ($P < 0.05$*; $P < 0.01$**; ND = no data).

3A). Although species richness in dry sites increased throughout the winter and spring, nearly twice as many species accumulated, on average, between January and April 2001 than in any other interval. In flowing sites, as in dry sites, species richness was reduced during the first postdrought sample ($t = -4.7$, $P = 0.03$), but the reduction was less than that observed in dry sites (Figure 3A).

In contrast, species richness in dry sites did not recover relative to flowing reference sites until 1 year after the drought. Species richness differed significantly among all sample groups (Table 3). Species richness was similar in dry and flowing sites during predrought sampling, significantly lower in dry sites than in flowing sites through June 2001, and similar again by November 2001 (Table 3; Figure 3A).

Catch Per Unit Effort

By June 2001, fish CPUE in dry sites was not significantly different from predrought levels. Fish CPUE in dry sites was extremely low during the first two postdrought samples and was significantly different from predrought levels until the June 2001 sample (paired, one-sided permutation t-tests: $t < -5.2$, $P < 0.01$ for significant tests; Figure 3B). Catch per unit effort began to increase in April 2001 and peaked in June 2001 (Figure 3B). In contrast, fish CPUE in flowing sites was about the same for the predrought period and for the first postdrought sample, but the June 2001 CPUE was significantly lower than predrought levels ($t = -4.7$, $P = 0.03$; Figure 3B).

Similarly, the CPUE in dry sites recovered relative to flowing sites by June 2001. Overall, CPUE differed significantly among all sample groups (Table 3). Immediately after the drought, CPUE was significantly lower in dry sites than in flowing sites, but by June 2001 CPUE was comparable between dry and flowing sites (Table 3; Figure 3B). In November 2001, CPUE was again significantly lower in dry sites than in flowing sites.

Fish Recolonization Patterns

The recolonization of the fish fauna at drought-affected sites was a highly ordered, nonrandom temporal process, as evidenced by significantly nested fish assemblages over time in six of the seven dry sites (Table 4). Observed T° values were far below the means of the randomly generated T° values (i.e., large σ) for the six sites (Table 4). Maximally packed matrices of dry sites were typically ordered with the predrought sample as the first row, followed by the remaining samples in reverse chronological order. Thus, after flows resumed, species incrementally accumulated over time in dry sites, and once a species recolonized a site its persistence was high. The only dry site that did not have a significantly nested assemblage pattern was D1. Because flows became intermittent at that site by June 2001, fish immigration to the site was prevented at least periodically during the summer, which would be expected to reduce nestedness over time. Matrix temperature was not significant for any flowing site, and it was higher (i.e., less ordered) than the randomly generated mean T° for four of the five flowing sites (Table 4). Thus, flowing sites did not show an ordered pattern of species presence over time.

TABLE 3.—Results of ANOVAs comparing species richness and catch per unit effort (CPUE fish/min) among sample groups during predrought (1999) and postdrought periods in northern Mississippi streams. All dry or flowing sites from one sample period constitute a sample group. Comparisons among all sample groups are followed by comparisons of samples from dry versus flowing sites for each sample period.

Sample groups compared	df	*F*	*P*-value
	Species richness		
Flowing versus dry, all groups[a]	7, 39	7.40	0.0000
Flowing versus dry, predrought	1, 10	4.72	0.0913
Flowing versus dry, Nov 2000	1, 10	33.04	0.0017
Flowing versus dry, Jun 2001	1, 10	6.35	0.0367
Flowing versus dry, Nov 2001	1, 9	3.37	0.0913
	CPUE		
Flowing versus dry, all groups[a]	7, 39	5.15	0.0007
Flowing versus dry, predrought	1, 10	0.02	0.8961
Flowing versus dry, Nov 2000	1, 10	12.60	0.0012
Flowing versus dry, Jun 2001	1, 10	0.02	0.7472
Flowing versus dry, Nov 2001	1, 9	7.07	0.0267

[a] Includes all samples from the four periods when both flowing and dry sites were sampled.

Immigration Probabilities

Fish species with the highest immigration probabilities were mostly headwater inhabitants or those documented as colonizing species (Figure 4; Appendix 1). Species that had the highest immigration probabilities (>0.45) and that also occurred at over half of the dry sites were creek chub, bluegills, green sunfish, blackspotted topminnow, and redspot darters. Of the five species that did not recolonize (immigration probability = 0), those with the highest predrought CPUEs were the Mississippi silvery minnow and the dusky darter (Appendix 1).

Species-specific immigration probabilities were associated with predrought species distributions and showed similarity between studies. Mean species-specific immigration probabilities were correlated with the number of sites occupied during the predrought period ($r = 0.50$, $n = 20$, $P < 0.01$) and with postdrought CPUE ($r = 0.70$, $n = 20$, $P < 0.01$) but not with predrought CPUE ($r = 0.07$, $n = 20$, $P = 0.40$). Mean species-specific

TABLE 4.—Nestedness matrix temperature (T°) values (with *P*-values), number of SD units (σ) by which observed T° diverged from the mean of randomly generated T° values for a site, percent fill of each matrix, and matrix size (number of samples × number of species). Matrices with *P*-values less than 0.05 were considered significant.

Site	T° (*P*)	σ	% Fill	Size
Dry sites				
D1	23.71 (0.068)	−1.50	48.7	5 × 16
D2	0.15 (0.006)	−2.53	50.0	6 × 6
D3	18.18 (0.004)	−2.70	40.7	6 × 18
D4	10.52 (0.005)	−2.61	42.4	6 × 11
D5	31.42 (0.043)	−1.72	44.4	6 × 27
D6	26.44 (0.008)	−2.43	52.0	5 × 25
D7	16.01 (0.004)	−2.70	37.9	6 × 18
Flowing sites				
F1	44.40 (0.820)	0.95	42.1	4 × 28
F2	36.55 (0.816)	0.94	49.2	3 × 32
F3	43.76 (0.841)	1.06	48.3	4 × 17
F4	52.11 (0.955)	1.82	45.4	4 × 28
F5	28.11 (0.156)	−1.02	59.7	4 × 23

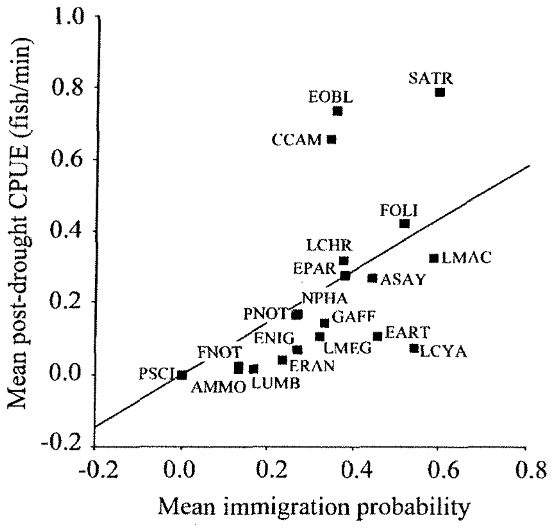

FIGURE 4.—Mean fish immigration probability by species in dry sites (during drought; see Methods) in northern Mississippi versus mean postdrought catch per unit effort (CPUE = fish caught/min of electrofishing) across all postdrought sample dates (November 2000–November 2001). Only species that occurred at more than one dry site during the predrought period are included. For each species, we calculated means based on only those sites where we captured the species at least once. The linear regression line is shown. Species abbreviations are given in Appendix 1.

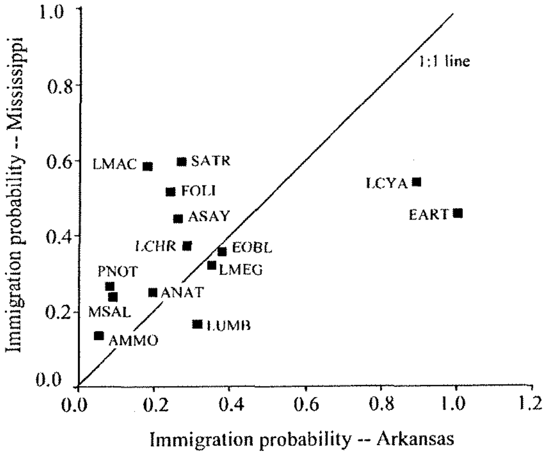

FIGURE 5.—Mean immigration probabilities for fish species in dry sites in northern Mississippi (this study) and in Arkansas (Taylor and Warren 2001). Species abbreviations are defined in Appendix 1.

immigration probabilities in our study were weakly associated with those from an Arkansas study (Taylor and Warren 2001) ($r = 0.42$, $n = 14$, $P = 0.06$; Figure 5). The green sunfish and redspot darter had high mean immigration probabilities in both studies but particularly so in the Taylor and Warren (2001) study, and yellow bullheads, largemouth bass, and lampreys had low immigration probabilities in both studies (Appendix 1).

Site-specific immigration probabilities were not correlated with predrought species richness or stream size (watershed area) ($r = -0.13$ and -0.49, respectively; $n = 7$, $P > 0.16$ for both), but the range of site-specific immigration probabilities was narrow (0.27–0.41). The sites with the two lowest site-specific immigration probabilities (D6 and D3) had relatively high predrought species richness and were over 1 km from a larger stream with flowing water during the drought. Of sites with the highest immigration probabilities, one (D2) was over 1 km from flowing water but had very low predrought richness, and the other (D5) had high predrought richness and may have maintained pools or minimal flow during the drought.

Mode of Fish Recolonization

Most fish that initially recolonized dry sites were at least age 1 (Figure 6A, B); these were followed later by smaller, mostly age-0, fish. In dry sites, the CPUE of large fishes (>4 cm TL) increased significantly by April 2001 and remained elevated relative to the first postdrought sample (paired, two-sided permutation *t*-test: $t > 3.0$, $P < 0.02$ for all significant tests; Figure 6B). Large-fish CPUE increased again in November 2001, presumably resulting from recruitment of age-0 fishes into the large size-class. The CPUE of small fishes (≤4 cm TL) also increased significantly by April in dry sites but increased much more dramatically from April to June, coincident with a peak in reproduction ($t > 2.2$, $P < 0.03$ for all significant tests; Figure 6A). Many small fish of numerous species were represented in dry sites in June 2001. In flowing sites, we found no differences in CPUE between the first and subsequent postdrought samples for either size-class (Figure 6C, D). Statistical power was lower in flowing sites, but nonetheless the trends in CPUE for small fish were in opposite directions for flowing and dry sites.

During the peak of the drought, we found 11 fish species in isolated water in or near the study reaches at four dry sites. Four species (blackspotted topminnow, western mosquitofish, green sunfish, and largemouth bass) persisted in pools at all four sites. However, during the first postdrought sample, western mosquitofish did not occur in any of the six sites that had definitely been desiccated, and the other three species occurred at one site each. Of the other species in isolated pools, three (creek chubsucker, longear sunfish, and creek chub) were found in one dry site in November 2000, and one (redfin shiner) did not reappear until April 2001. Three species (bluntface shiner, redspot darter, and bluntnose minnow) persisted in a short, isolated spring flow downstream of site D1, but none of these species reappeared in site D1 before April 2001.

Crayfish

We collected 2,002 crayfish representing at least seven species (Appendix 2). *Orconectes* sp. cf. *chickasawae* was the most widespread species as it occurred in all sites, and was the most abundant species in all but one predrought sample.

Crayfish relative density in dry sites approached predrought levels by April 2001 (Figure 7). Within dry sites, relative density was significantly lower in November 2000 and January 2001 than during the predrought period (paired, two-sided *t*-tests: $t < -1.6$, $P < 0.04$; Figure 7). Crayfish relative density in dry sites increased continuously and peaked in June 2001 at a level that was significantly higher than the predrought density ($t = 5.4$, $P < 0.02$). Although relative densities in most dry sites declined from June to November 2001, they remained higher than densities observed in November 2000 ($t = 3.3$, $P < 0.02$). Flowing sites

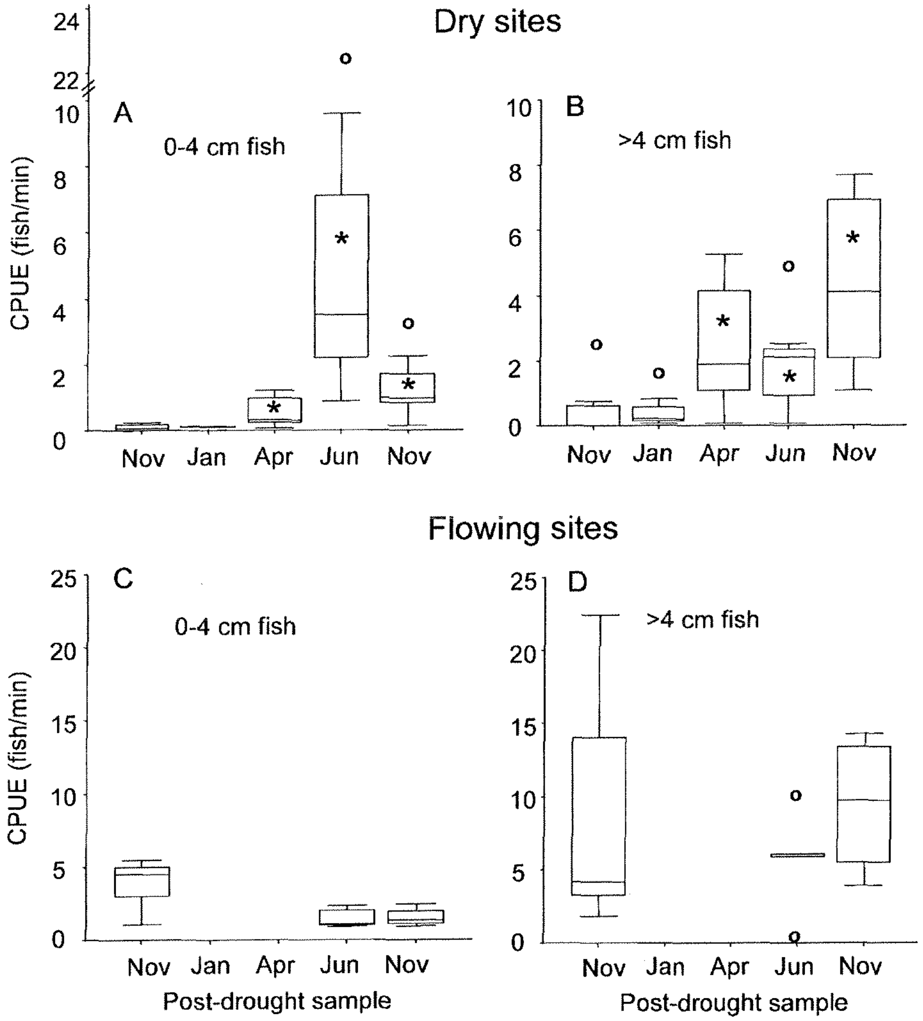

FIGURE 6.—Box plots of postdrought catch per unit effort (CPUE = fish/min) for fish sampled during November 2000–2001, as follows: (A) fish 4 cm or less, sampled at dry sites, (B) fish over 4 cm, sampled at dry sites, (C) fish 4 cm or less, sampled at flowing sites, and (D) fish over 4 cm, sampled at flowing sites. Plots indicate median, interquartile range, and outliers (values > 1.5 times interquartile range; circles). Asterisks in boxes indicate a significant difference ($P < 0.05$) in CPUE in a given sample relative to the first postdrought sample. In panel B, all outliers were from one site (D5) where a small amount of flow may have occurred throughout the drought (ND = no data).

showed no significant differences in crayfish relative density over time (Figure 7).

Overall, crayfish relative density differed significantly among all sample groups (dry and flowing sites; ANOVA: $F = 4.13$; df = 7, 36; $P < 0.003$; Figure 7). The relative density in dry sites was similar to that in flowing sites during the predrought period, was significantly lower than the flowing-site density immediately after the drought (November 2000; randomized ANOVA: $F = 22.0$; df = 1, 9; $P < 0.01$), and was significantly higher than flowing-site density by June 2001 (randomized ANOVA: $F = 5.2$; df = 1, 9; $P < 0.04$; Figure 7). Relative densities were again similar between dry and flowing sites in November 2001.

Recovery of crayfish size structure was not as rapid as the recovery of relative density. By June 2001, crayfish sizes remained significantly smaller than those in predrought samples at dry sites but not at flowing sites (Figure 8A). In June 2001, the proportion of crayfish in the 0.0–2.5-cm size-class was significantly greater than predrought propor-

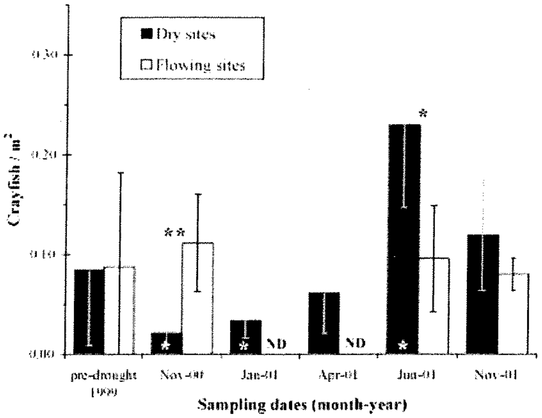

FIGURE 7.—Crayfish relative density (number/m^2) in predrought (summer 1999) and postdrought (November 2000–November 2001) samples in northern Mississippi streams. Crayfish of all species and sizes captured by electrofishing and seining are included. Asterisks above bars indicate significant differences between dry and flowing sites (ANOVA). Asterisks at the bottom of a bar indicate significant differences between that sample group and the predrought group in the same category (paired, two-sided *t*-test: ($P < 0.05$*; $P < 0.01$**; ND = no data).

tions in every dry site (Figure 8A; paired *t*-test: $t = 2.98$, $P = 0.009$). Concurrently, relative densities of the largest crayfish (>5 cm) remained lower than predrought densities in all dry sites, but small sample sizes precluded statistical testing (Figure 8A). In flowing sites in June 2001, the proportion of crayfish in the smallest size-class was not significantly different than the predrought proportion, having increased in two sites and decreased in two others (paired *t*-test: $t = -0.31$, $P = 0.679$; Figure 8B).

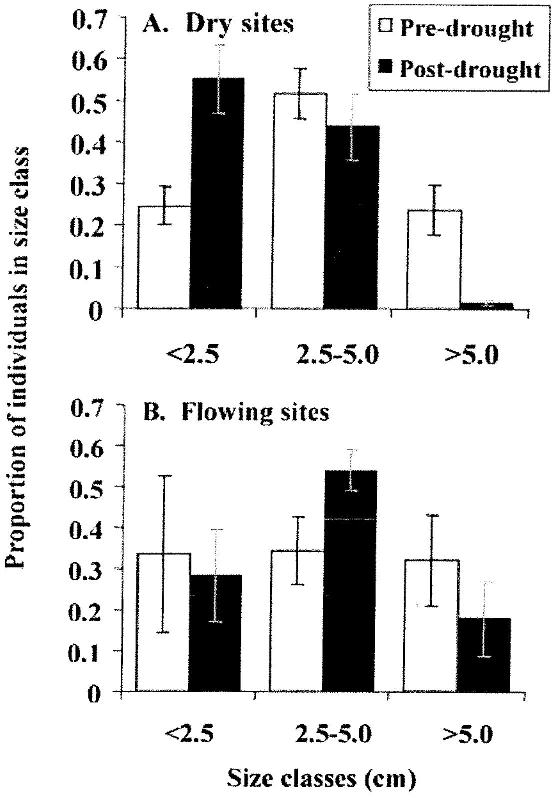

FIGURE 8.—Mean (±2 SEs) proportions of individual crayfishes in three size-classes during predrought (summer 1999; see Table 1 for dates) and postdrought (June 2001) periods in (**A**) dry sites ($n = 7$) and (**B**) flowing sites ($n = 4$). Sizes are body lengths, and both electrofishing and seining data are included.

Discussion

Fish recolonization of stream reaches desiccated by drought was initially slow during winter but became increasingly rapid in spring and early summer. Thus, it was not until months after flows resumed that we saw the rapid recolonization rates typically observed immediately after disturbance in previous studies. By June 2001 (6–7 months after flows resumed), the overall fish assemblage structure, CPUE, and species richness in dry sites were no longer significantly different from those recorded prior to stream drying. We documented that recolonization resulted from a combination of immigration and reproduction, partially due to the timing of disturbance relative to the reproductive cycle. Because annual and seasonal variability in fish assemblage structure is extremely high in the region (Shields et al. 1995; Adams et al. 2004), defining a particular point that represents numerical recovery is not feasible without a long time series of predrought assemblage data.

The initially slow recolonization contrasts with other reports of rapid (days to weeks) initial recolonization after experimental defaunations or human-caused spring or summer fish kills (Larimore et al. 1959; Olmsted and Cloutman 1974; Bayley and Osborne 1993; Peterson and Bayley 1993; Sheldon and Meffe 1995; Lonzarich et al. 1998). Larimore et al. (1959) observed rapid recolonization after drought, but full flows resumed in April rather than in fall, so seasonal effects were confounded by hydrologic factors. The delay we observed in recolonization strongly supports the long-standing hypothesis that recolonization rates depend on season and timing with respect to species-specific life histories (Larimore et al. 1959; Olmsted and Cloutman 1974; Niemi et al. 1990; Detenbeck et al. 1992). In addition, our observations during seining indicated that aquatic insect densities during the first postdrought sample (November 2000) were dramatically lower in dry streams than in flowing streams, so food may have been limiting at that time.

The strong seasonal component of immigration over relatively large scales is consistent with a highly mobile community in which many species make long-distance seasonal movements within stream networks. Schlosser (1987) proposed that such mobility should characterize fish assemblages in headwater and disturbed streams, such as the ones in this study. Many warmwater stream fishes undergo long-distance upstream migrations related to reproduction in spring or early summer (Funk 1955; Larimore et al. 1959; Hall 1972; Whitehurst 1981), consistent with the pattern of recovery we observed. Further, declines in CPUE from June to November 2001 may reflect seasonal movements out of smaller streams (Larimore et al. 1959; Olmsted and Cloutman 1974) as well as mortality. Perhaps more intriguing than the high degree of spring movement was the late fall–early winter immigration, albeit limited, of fishes into sites that had been completely desiccated and that were over 1 km from perennial water bodies. Virtually nothing is known about the proximal cues that induce long-distance upstream movements by fishes during periods of typically low mobility.

The recolonization process by fish was highly ordered, as reflected in the nested species pattern wherein the early postdrought assemblages consisted of subsets of the species that occurred prior to the drought and during the summer after the drought. This contrasts with flowing streams, in which species were not nested over time. Similarly, small Arkansas streams with high variability in flow had stronger nested patterns over time than did larger, more hydrologically stable streams (Taylor and Warren 2001).

The change in CPUE of small (mostly age-0) individuals over time provided evidence that reproduction was a fundamental component of postdrought assemblage recovery. The pattern of species richness initially increasing more rapidly than abundance has been observed fairly consistently in fish recolonization studies (Detenbeck et al. 1992; Lonzarich et al. 1998), and in our study the pattern resulted from early immigration by relatively few, primarily adult, individuals of many species, subsequent reproduction, and continued immigration. Because populations upstream of most dry sites were either eliminated by the drought or were separated from a given site by an intervening reservoir, we infer that much of the reproduction was in situ; it seems unlikely that large numbers of age-0 fish ($\leq$4 cm TL) immigrated from downstream. Larimore et al. (1959) also showed that reproduction contributed greatly to numerical recovery of most, but not all, fish species after a drought. Bayley and Osborne (1993) hypothesized that biomass recovery in desiccated streams was due in large part to in situ production rather than to immigration, because they found no evidence of fish becoming concentrated downstream in flowing streams during the drought. In contrast to our findings, recolonization after a May fish kill in Arkansas was characterized initially by rapid immigration of predominantly age-0 and immature individuals (Olmsted and Cloutman 1974); however, most colonists were thought to be immigrating from upstream rather than downstream, and the seasonal timing differed from that observed in our study.

Species whose postdrought CPUEs were well above the regression line for immigration probability and postdrought CPUE (i.e., bluntface shiner, creek chubsucker, and creek chub) may be particularly dependent on reproduction for their rapid numerical recovery. Because immigration probabilities were based on presence–absence data, they were not inherently related to CPUE; therefore, a species' location on the plot potentially provides insight into mechanisms of recolonization. Numbers of large versus small fish are consistent with the idea that the numerical recovery of creek chubsuckers and creek chub was driven largely by reproduction; however, the pattern did not hold for bluntface shiners. The five species above the regression line belong to four of the six reproductive guilds described by McCormick et al. (2001), including broadcast spawner, egg attacher, clean gravel spawner, and nest associate. From this, we see no obvious relationships between reproductive guild and ability to recolonize after disturbance (as suggested by Ensign et al. 1997), despite the fact that recruitment played a clear role in numerical recovery.

Although refuge pools persisted in or near four dry sites, the pools were apparently not a major source of colonists when flows resumed. In fact, few of the species that dominated isolated pools appeared at all in the first postdrought samples. Our observations support Larimore et al.'s (1959) suggestion that the "stagnant-water forms" dominating even nonstagnant, isolated stream pools during drought are not necessarily well adapted for recolonizing streams when flows resume.

Predrought fish distribution was related to species-specific immigration probabilities, but predrought CPUE was not; however, numerous species with low immigration probabilities did have low mean values of predrought CPUE. Other studies have demonstrated relationships between predisturbance abundance and postdisturbance immigration or recolonization (Sheldon and Meffe 1995; Taylor and Warren 2001), but Larimore et al. (1959) did not find such a relationship. Several explanations for the relationships we observed are possible. Widespread species may have higher potential to reach high abundances and increase their persistence when conditions are favorable, such as during postdisturbance periods when fish assemblages are simplified and densities are low; however, biotic factors limit the abundances of such species during more stable conditions (Schlosser 1987; Poff and Ward 1990). Predrought abundance may be irrelevant to recovery for headwater fishes if most are eliminated during a drought. Headwater fishes that move down to larger streams during stream drying may suffer high mortality from predation or other factors and may not be available to recolonize after a drought. This is consistent with the lack of crowding in downstream habitats during severe drought in Illinois; crowding would be expected if headwater fishes migrated downstream and survived (Bayley and Osborne 1993). Postdrought immigration probability may be more weakly linked to predisturbance abundance in studies conducted over larger, longer scales than are typical of defaunation studies (e.g., Sheldon and Meffe 1995) or in studies where disturbance is more atypical than the annual drying in intermittent streams (e.g., Taylor and Warren 2001). Finally, the lack of correlation between immigration probability and predrought CPUE may result in part from the 12–15-month time lag between predrought sampling and stream desiccation.

Given the numerous factors that can influence recolonization, the similarities among studies in terms of recolonization by individual species are particularly compelling. For example, species-specific immigration probabilities in this study and the study in Arkansas (Taylor and Warren 2001) shared many similarities despite numerous ecosystem differences, including much more gradual channel slopes and unstable channel substrates in the Mississippi streams. Consistent with nearly all previous studies, we observed rapid recolonization ability in many cyprinids (Larimore et al. 1959; Detenbeck et al. 1992; Bayley and Osborne 1993; Sheldon and Meffe 1995) but also in members of Centrarchidae (Detenbeck et al. 1992; Bayley and Osborne 1993; Sheldon and Meffe 1995), Catostomidae, Aphredoderidae, Fundulidae, and Percidae (Larimore et al. 1959). The blackspotted topminnow, creek chub, striped shiner, golden shiner (Olmsted and Cloutman 1974), and bluntnose minnow (Larimore et al. 1959; Olmsted and Cloutman 1974) recolonized relatively quickly in this and other studies. The blackstripe topminnow was a slow recolonizer in our study and other studies, in contrast to its sister species, the blackspotted topminnow (Larimore et al. 1959; Matthews and Marsh-Matthews 2003), which may help explain why the blackstripe topminnow is the less widespread of the two species in small streams of northern Mississippi. During this study, the dusky darter had an immigration probability of zero in dry sites and also disappeared from the two smallest flowing sites, which it failed to recolonize. The dusky darter appears to be particularly susceptible to drought effects other than complete cessation of surface flow (Hubbs and Hettler 1958), and populations may have been eliminated for a considerable distance from even those dry sites located near flowing water.

For a number of other species, our results differed dramatically from those of other studies. In contrast to Olmsted and Cloutman (1974) but similar to Larimore et al. (1959), we found that the bluegill and green sunfish were the first *Lepomis* spp. to recolonize, whereas the longear sunfish was slow to immigrate and recolonize. No catostomids were "significantly reestablished" after 1 year in Arkansas streams (Olmsted and Cloutman 1974), but we found that the creek chubsucker recolonized fairly rapidly. The yellow bullhead was a late arriver and slow recolonizer in Arkansas streams (Olmsted and Cloutman 1974), but we observed moderate recovery of the species by early summer. The redfin shiner was the fastest postdrought recolonizer in Illinois (Larimore et al. 1959) but was very slow to recolonize streams in our study. Such differences in recolonization may reflect habitat conditions, biotic interactions, size and distribution of source populations, and perhaps an element of chance.

Crayfish

The patterns of numerical recovery in crayfish were similar to those in fishes except that crayfish populations increased slightly more rapidly than fish populations during winter. Also, postdrought crayfish densities in June 2001 exceeded predrought levels in all dry sites and some flowing sites. Although virtually no ecological research has been done on the species that were common in this study, some other crayfishes appear to have either high resistance or resilience to both supraseasonal and periodic drought. In Georgia streams that were partially desiccated by drought, relative abundances of adult *Procambarus spiculifer*, a tertiary burrower (as are at least several species in this study), were depressed during and immediately after two droughts but returned to predrought levels 2–3 years after the first drought (Taylor 1983, 1988). Larimore et al. (1959) noted that crayfish abundances increased in many stream pools from April to July after a supraseasonal drought. Conversely, densities of the crayfish *Paranephrops planifrons* were reduced for nearly 3 years after a major flood in a New Zealand stream (Parkyn and Collier 2004); however, initial densities were much higher than in our study, and *P. planifrons* matures later than the species we studied and does not burrow.

More detailed studies are needed to determine how crayfish species with different burrowing habits, trophic interactions, and population dynamics respond to drought (Taylor 1983). Densities of two *Orconectes* spp. were higher in intermittent streams than in permanent streams in the Ozark Plateau, but densities of two others did not differ between stream types (Flinders and Magoulick 2003). Some other *Orconectes* spp. require permanent water (Hamr 2002), whereas some *Procambarus* spp. thrive in habitats that are seasonally dewatered (Huner 2002).

Momot (1966) stated that crayfish "repopulate streams by upstream migration rather than by reproduction in situ"; however, we found that for populations recovering from supraseasonal drought, in situ reproduction may be an important mechanism of recovery. Crayfish size distributions shifted toward smaller individuals after the drought in all dry sites, reflecting successful postdrought reproduction as well as lower numbers of large adults. *Procambarus spiculifer* populations also had smaller mean body sizes and increases in juvenile–adult ratios during a drought and for at least 2 years afterward (Taylor 1988). The changes in *P. spiculifer* population size structure resulted from the loss of the largest individuals in two sites, coupled with an increase in juveniles in one site during the drought. Caine (1978) observed smaller mean body sizes of *Procambarus* spp. in regularly drying habitats than in nondrying habitats in Florida, but Flinders and Magoulick (2003) did not find this pattern for *Orconectes* spp. in Ozark streams. *Paranephrops planifrons* in New Zealand appeared to recover from flood-induced population reductions via reproduction of surviving crayfish rather than by immigration, although few source populations remained to provide recolonizers (Parkyn and Collier 2004). Reduced predation pressure from fish and larger crayfish may have led to increased survival of juvenile crayfish after the drought in our study (Huner 2002; Flinders and Magoulick 2003). The lower density of large individuals after the drought may have been caused by drought-induced emigration and mortality. Larimore et al. (1959) observed crayfish leaving isolated stream pools after the pools became putrid during severe drought, and Caine (1978) noted a bias toward higher mortality of larger *Procambarus paeninsulanus* during drying experiments.

Management Implications

Though fish and crayfish assemblages were apparently well adapted to repopulating headwater streams after disturbance, the effects of the drought continued to influence the assemblages 1 year later. Species that recolonized slowly or not at all during this study may be useful indicators of postdisturbance recovery or of habitats that are relatively stable. For example, abundant dusky darters, redfin shiners, and lamprey ammocoetes at a site may indicate that flow has not ceased or has reached some minimum level for at least several years. Longer-term investigations will be required to determine which species are consistent indicators of complete recovery in the region.

A critical implication of the resilient fish communities and the associated high mobility of their members is that effective management must ensure the ability of fish to move freely throughout stream networks, especially during times of high seasonal movements and extreme stress (e.g., drought). Furthermore, research designed to understand population processes over scales larger than a single reach and over multiple seasons are sorely needed for most southeastern U.S. stream fishes.

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Appendix 1: Fish Species in Study

TABLE A.1.—Species names, abbreviations, families, and total counts (from electrofishing and seining) of fish from predrought (pre) versus postdrought (post) samples grouped by dry sites (n = 7) versus flowing sites (n = 5) in northern Mississippi streams. Numbers of individuals caught predrought represent one sample (summer 1999), whereas numbers caught postdrought are sums from five sample dates in dry sites and three dates in flowing sites (two at site F2; see Table 1). Species' mean immigration probabilities (SD) were calculated only from dry sites where the species occurred at least once. Lampreys were identified to genus and species only in late winter and early spring, when adults were present.

Family	Species	Species code	Immigration probability
Aphredoderidae	Pirate perch *Aphredoderus sayanus*	ASAY	0.44 (0.19)
Atherinidae	Brook silverside *Labidesthes sicculus*	LSIC	
Catostomidae	Creek chubsucker *Erimyzon oblongus*	EOBL	0.36 (0.14)
	Northern hog sucker *Hypentelium nigricans*	HNIG	
	Blacktail redhorse *Moxostoma poecilurum*	MPOE	
Centrarchidae	Green sunfish *Lepomis cyanellus*	LCYA	0.54 (0.36)
	Warmouth *Lepomis gulosus*	LGUL	0.22 (0.04)
	Bluegill *Lepomis macrochirus*	LMAC	0.58 (0.25)
	Dollar sunfish *Lepomis marginatus*	LMAR	0.25 (na)
	Longear sunfish *Lepomis megalotis*	LMEG	0.32 (0.11)
	Redear sunfish *Lepomis microlophus*	LMIC	0.00 (na)
	Spotted bass *Micropterus punctulatus*	MPUN	
	Largemouth bass *Micropterus salmoides*	MSAL	0.24 (0.02)
	White crappie *Pomoxis annularis*	PANN	
Clupeidae	Gizzard shad *Dorosoma cepedianum*	DCEP	
Cyprinidae	Bluntface shiner *Cyprinella camura*	CCAM	0.34 (0.15)
	Blacktail shiner *Cyprinella venusta*	CVEN	0.10 (0.14)
	Cypress minnow *Hybognathus hayi*	HHAY	
	Mississippi silvery minnow *Hybognathus nuchalis*	HNUC	0.00 (na)
	Striped shiner *Luxilus chrysocephalus*	LCHR	0.38 (0.18)
	Ribbon shiner *Lythrurus fumeus*	LFUM	
	Redfin shiner *Lythrurus umbratilis*	LUMB	0.17 (0.16)
	Golden shiner *Notemigonus crysoleucas*	NCRY	0.28 (0.05)
	Emerald shiner *Notropis atherinoides*	NATH	0.00 (na)
	Yazoo shiner *Notropis rafinesquei*	NRAF	1.00 (na)
	Mimic shiner *Notropis volucellus*	NVOL	0.25 (na)
	Pugnose minnow *Opsopoeodus emiliae*	OEMI	0.25 (0.00)
	Bluntnose minnow *Pimephales notatus*	PNOT	0.27 (0.07)
	Creek chub *Semotilus atromaculatus*	SATR	0.60 (0.29)
Esocidae	Redfin pickerel *Esox americanus*	EAME	
Fundulidae	Blackstripe topminnow *Fundulus notatus*	FNOT	0.13 (0.16)
	Blackspotted topminnow *Fundulus olivaceus*	FOLI	0.52 (0.34)
Ictaluridae	Yellow bullhead *Ameiurus natalis*	ANAT	0.25 (0.00)
	Channel catfish *Ictalurus punctatus*	IPUN	
	Brindled madtom *Noturus miurus*	NMIU	
	Brown madtom *Noturus phaeus*	NPHA	0.27 (0.04)
	Flathead catfish *Pylodictis olivaris*	POLI	
Lepisosteidae	Spotted gar *Lepisosteus oculatus*	LOCU	
Percidae	Redspot darter *Etheostoma artesiae*	EART	0.46 (0.31)
	Bluntnose darter *Etheostoma chlorosoma*	ECHL	0.25 (na)
	Slough darter *Etheostoma gracile*	EGRA	
	Harlequin darter *Etheostoma histrio*	EHIS	
	Brighteye darter *Etheostoma lynceum*	ELYN	0.00 (na)
	Johnny darter *Etheostoma nigrum*	ENIG	0.27 (0.04)
	Goldstripe darter *Etheostoma parvipinne*	EPAR	0.38 (0.22)
	Cypress darter *Etheostoma proeliare*	EPRO	0.50 (0.24)
	Yazoo darter *Etheostoma raneyi*	ERAN	0.23 (0.07)
	Gulf darter *Etheostoma swaini*	ESWA	0.25 (na)
	Dusky darter *Percina sciera*	PSCI	0.00 (0.00)
	River darter *Percina shumardi*	PSHU	
Petromyzontidae	*Ichthyomyzon* lamprey *Ichthyomyzon* sp.	ISPP	
	Least brook lamprey *Lampetra aepyptera*	LAEP	
	Unknown lamprey ammocoete	AMMO	0.13 (0.12)
Poeciliidae	Western mosquitofish *Gambusia affinis*	GAFF	0.33 (0.14)
Sciaenidae	Freshwater drum *Aplodinotus grunniens*	AGRU	
Total			

TABLE A.1.—Extended.

Family	Dry		Flowing		
	Pre	Post	Pre	Post	Total
Aphredoderidae	2	56	9	47	114
Atherinidae			6	2	8
Catostomidae	7	271	9	31	318
			13	12	25
			5	6	11
Centrarchidae	23	19	6	6	54
	2	5	4	9	20
	99	144	89	430	762
		1	2		3
	24	37	23	51	135
	2				2
			25	20	45
	1	14	2	16	33
			5	12	17
Clupeidae			4		4
Cyprinidae	115	167	161	658	1,101
	2	1	73	153	229
			1		1
	27		1		28
	14	67	2	12	95
		1	3		4
	74	6	8	56	144
	1	20		31	52
	7		58	13	78
	8	164	14	372	558
		2	8	7	17
		2		6	8
	69	71	5	99	244
	139	503	6	78	726
Esocidae				1	1
Fundulidae	9	6	8	14	37
	63	216	53	445	777
Ictaluridae	1	15	3	6	25
			2	2	4
			2	2	4
	13	48	53	98	212
			2		2
Lepisosteidae			1		1
Percidae	17	54	2	18	91
		3			3
		1		1	2
				6	6
	3		65	82	150
	3	23	3	36	65
	65	138	9	18	230
		26	1	4	31
	11	16	17	64	108
	1	3	5	2	11
	18		54	51	123
			2		2
Petromyzontidae				1	1
		3		44	47
	13		38	43	94
Poeciliidae	12	37		30	79
Sciaenidae				1	1
Total	845	2,140	862	3,096	6,943

Appendix 2: Crayfish Species in Study

TABLE A.2.—Crayfish species identified from northern Mississippi stream sites 1999–2001 (D = sites that were dry during the drought, F = flowing sites). Note that most individuals in postdrought samples were not collected or identified to species. *Orconectes* sp. cf. *chickasawae* appears to be an undescribed species that closely resembles *O. chickasawae* (S.B.A., unpublished data).

	Site											
Species	D1	D2	D3	D4	D5	D6	D7	F1	F2	F3	F4	F5
Cambarus diogenes						X	X					
Cambarus sp.										X		
C. striatus	X	X	X	X			X	X				X
Fallicambarus sp.	X											
Orconectes sp. cf. *chickasawae*	X	X	X	X	X	X	X	X	X	X	X	X
Procambarus hayi	X			X	X	X	X					X
P. ouachitae						X						X
P. vioscai			X		X			X	X		X	X
Procambarus sp.						X						