Effects of Summer Drought on Fish and Macroinvertebrate Assemblage Properties in Upland Ouachita Mountain Streams, USA

JOSEPH W. LOVE[1]

NOAA Living Marine Resources Cooperative Science Center, University of Maryland Eastern Shore, Princess Anne 21853

CHRISTOPHER M. TAYLOR

Mississippi State University, Department of Biological Sciences, Mississippi State 39759

AND

MELVIN P. WARREN, JR.

U.S.D.A. Forest Service, Oxford Laboratory, Oxford, Mississippi 38655

ABSTRACT.—We sampled fishes and aquatic insects monthly (Jun.–Sept. 2002) from intermittent tributaries of the Alum Fork of the Saline River (Arkansas, U.S.A.) to quantify the response of fish and aquatic insect assemblage properties to seasonal desiccation and habitat fragmentation. We collected a total of 4219 individuals, representing 18 species of fishes and 27 families of aquatic insects. Changes in the composition of fish assemblages were significantly related to temporal variability in pool volume and location in the watershed. Smaller, upstream pools varied in volume more than downstream pools. Fish assemblages were significantly more similar through summer in downstream, larger pool habitats. Changes in the composition of aquatic insect families were related to variation in water quality conditions. Highly eutrophied sites were typically dominated by midge larvae (Chironomidae), resulting in highly similar assemblages over time. Our results support findings at larger space and time scales and call attention to the importance of rapid changes in habitat quality, size and connectivity on stream communities.

INTRODUCTION

It is generally understood that fish assemblage variability in streams is spatially structured (*see* Matthews, 1998; Taylor *et al.*, 2006), with higher flow variability in upstream reaches corresponding to increased assemblage variability and higher local extinction rates (Grossman *et al.*, 1982; Gotelli and Taylor, 1999; Taylor and Warren, 2001). Schlosser (1982, 1985) has suggested that physical processes affecting habitats, such as periodic spates and drought, influence fish assemblages by altering local reproductive success and
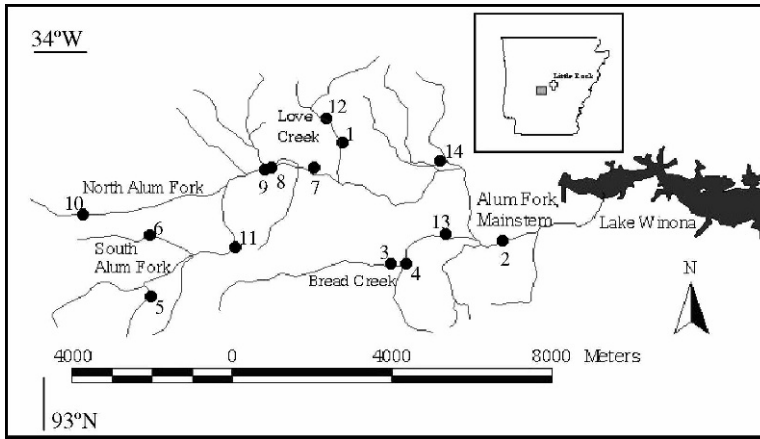
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[1] Email: jlove@umes.edu

FIG. 1.—Map of 14 study sites in tributaries of the Alum Fork of the Saline River drainage in central Arkansas (Jun.–Sept., 2002)

recolonization rates. Even though such patterns of assemblage variability within watersheds have been shown at coarser scales of resolution (stream reaches encompassing multiple habitats), across years and seasons (Taylor and Warren, 2001; Williams *et al.*, 2003), intraseasonal dynamics related to unpredictable spates and habitat desiccation in intermittent streams during summer are not well-known (Magoulick and Kobza, 2003).

During the summer, flow in intermittent streams in the Ouachita Mountains, Arkansas is typically reduced, resulting in aquatic assemblages that are isolated in pools when riffles dry (Taylor and Warren, 2001). Pool drying results in an increased density of both macroinvertebrates (Miller and Golladay, 1996) and fishes (Williams *et al.*, 2003), and may cause the localized extinction of less abundant species. Pools progressively dry and deteriorate until flow is re-established by periodic spates. The interaction between the extent of summer spates and pool drying, and the spatial position of sites within the drainage is unclear, but should result in higher assemblage variability and extinction rates in small, upstream pools (Taylor, 1997; Gotelli and Taylor, 1999). Downstream pools are likely to exhibit lower assemblage variability because of higher immigration rates from larger, neighboring populations and more benign environmental conditions (Taylor and Warren, 2001).

In this paper, we investigated how important environmental gradients during summer drought affected local fish and aquatic insect assemblages. We predicted that assemblage variability for both fishes and aquatic insects would be positively associated with hydrologic disturbance. Assemblage variability ultimately results from differences in immigration and extinction (or emigration) events. At the species level, we predicted that species-specific immigration and extinction rates would correspond positively and negatively (respectively) to local abundance. For two common fish species in the system, we examined changes in body condition across time. We predicted that the stress of seasonal drought would adversely affect body condition, leading to a significant decline through time.

METHODS

STUDY AREA

We sampled 14 pools in the Alum Fork of the Saline River drainage monthly from Jun. to Sept. in 2002 (Fig. 1). Habitats included first to third order stream localities and included a

wide range of environmental variation. These streams are annually subjected to severe dry-down during summer and early fall (Jul.–Oct.) when precipitation is less frequent. As a result, isolated pools form allowing for a well-defined survey of pool assemblages and habitat characteristics.

Environmental variables were measured during midday (1000–1400) during each pool survey. Dissolved oxygen (DO), specific conductivity and temperature were measured using a Yellow Springs Instrument Model 85 (YSI-85). Chlorophyll *a* and turbidity were measured using a handheld flurometer (Turner Designs) as the average of three random samples. The pH at each site was measured using a Corning M90 pH Sensor. Pool volume was calculated as the product of length of the pool, mean pool width (n = 4, equally spaced transects) and mean pool depth (n = 16, 4 equally spaced points per transect). Depth was taken at 4 equidistant points along the same transect each month, unless pool drying required our randomly choosing another transect. Habitat variables were averaged across months and coefficients of variation (CVs) were calculated. The CV represented the magnitude of change in a variable at a site across time. With the exception of pH, all environmental variables were log transformed prior to analyses.

Sites were geo-referenced with a GPS Magellan handheld unit and entered into a spatial database created using ArcView (Version 3.2, Environmental Systems Research Institute, Inc., 1999). Spatial data of the watershed were obtained from GIS Data Depot (www.gisdatadepot.com) and the U.S.D.A. Forest Service. The shortest stream distance of each sampling site from the most downstream locality was calculated to quantify a pool's relative position in the watershed.

Aquatic insect collection.—We collected macroinvertebrates (Jul.–Sept.) using Hester-Dendy plate samplers (Hester and Dendy, 1962) and D-frame sweep nets. The plate samplers specifically target certain taxa (Ephemeroptera, Plecoptera, Trichoptera) (Rinella and Feminella, 2005), so we used D-frame sweep nets to improve collection of aquatic insects (Turner and Trexler, 1997). Samplers were randomly placed within each pool in Jun., with the last plate flush with substrate. Metal rods (0.95 cm diam, 61 cm long rebar) were driven into the stream bed and samplers were fitted to them with cable ties. The number of samplers depended on pool size with generally one sampler installed per 10 m^3 of volume. While samplers added habitat to the pools, the proportion of habitat added, relative to pool size, was consistent throughout the study period, making temporal comparisons in population sizes possible. Samplers remained in pools for one month to achieve colonization by macroinvertebrates (Crowe, 1974). In addition to plate samplers, we used a D-frame sweep net and made six, 10 s sweeps of all available microhabitats within each pool. We also recorded the presence of aquatic insect taxa that were observed on the surface of the water, but not collected during each sampling event (*e.g.*, Gyrinidae). We included these data into a presence-absence matrix (*see* below). Our sampling of macroinvertebrates likely excluded several important taxa within each pool, and our procedure provided insight into how some populations responded to water quality and hydrologic variability throughout summer.

All invertebrate samples were stored in 70% ethanol mixed with Rose Bengal dye to stain living tissue. We identified specimens to family and to genus when possible using Merritt and Cummins (1984). An archived reference collection of specimens is maintained at Mississippi State University. Analyses were performed at the family level to include specimens that were not identifiable to genus. The interpretation of results may be similar across taxonomic scales for many aquatic insects (Bowman and Bailey, 1997). Because the level of taxonomic resolution differed, however, we did not make specific comparisons of results for macroinvertebrate and fish assemblages.

Fish collection.—We used Gee minnow traps (3 cm diam opening) to sample fishes from Jun.–Sept. Number of traps varied by initial pool size (1 per 10 m^3 of volume) and remained constant throughout summer. A plastic, floater trap was also used at each site to improve the collection of surface-oriented and water-column fishes (*e.g.*, *Lythurus umbratalis*). The spatial distribution of Gee minnow traps may affect catchability of fishes (He and Lodge, 1988). Therefore, we placed traps in each pool along the same transects each month. We sampled fishes for 24 h, identified them to species, marked them by clipping the upper caudal lobe, measured them for standard length (Hubbs and Lagler, 2004) and weighed them (portable hand scale, Ohaus HP320, ±0.1 g). We released fish to their pool, rotated and re-set traps for another 24 h. Fishes were again sampled, identified and measured. We noted recaptures on the following day and excluded them from analyses. In addition, we recorded the presence of fish species that were observed but not collected, and included these data in analyses utilizing occurrence data (*see* below). In total, we sampled aquatic habitats for a 48 h period using a methodology that did not differ over time. While minnow traps are biased for species (Jackson and Harvey, 1997), our consistent sampling methodology allowed us to make temporal comparisons at a pool throughout summer. We limited our interpretations to those species that were selectively captured.

Data analyses.—We estimated temporal changes in assemblage structure from occurrence and relative abundance data (Lienesch *et al.*, 2000). We used occurrence data in addition to relative abundance data because relative abundances may have been underestimated using either plate samplers or minnow traps (*see* above). Occurrences were tabulated in presence-absence matrices for fishes and macroinvertebrates. We used occurrence data to calculate Jaccard's index of similarity (JI), which ranged from zero to one at a site, indicating completely dissimilar assemblages to identical assemblages across time, respectively. We used relative abundance data to calculate percent similarity indices (PSI), which also ranged from zero to one. Percent similarity was estimated by calculating Bray-Curtis distances and then subtracted from one. Similarity indices were calculated for all pairwise monthly samples at a locality and averaged to indicate overall assemblage variability.

We calculated extinction and immigration rates of fishes and aquatic insects following Taylor and Warren (2001). Extinction was defined as the absence of a species, whether due to extirpation or emigration, immediately following its presence during a previous census (Taylor and Warren, 2001). Briefly, immigration and extinction rates are probabilities derived from a presence-absence matrix. The probability of extinction (P_e) is the number of times a site was occupied at time (t), but unoccupied at time step (t + 1), divided by the number of times a site was occupied at t. The probability of immigration (P_i) is the number of times a site was unoccupied at t, but occupied at t + 1, divided by the number of times a site was unoccupied at t. We calculated these rates for the lowest level of taxonomic resolution of fishes and insects. We averaged P_i or P_e across taxa for each site. Analysis of variance (ANOVA) was used to test the null hypothesis of no difference between P_i and P_e across the landscape for fish and aquatic insect assemblages.

We determined how assemblage similarity and P_i and P_e were influenced by environmental gradients associated with stream drying using redundancy analysis (RDA). Redundancy analysis is a direct gradient analysis that relates predictor variables to response variables using a linear model of relationship between the variables (ter Braak, 1994; Makarenkov and Legendre, 2002). The resulting RDA axes represent gradients of the response variables as constrained by predictor variables. This analysis is usually undesirable for community datasets because of the assumption of linearity between response and predictor variables (Legendre and Anderson, 1999; McCune and Grace, 2002). The indices

we included as a response variable were fish and aquatic insect assemblage similarity indices, and P_i and P_e, which were not unimodally distributed. Predictor variables included environmental variables and their CVs. Vectors of predictor variables that were highly correlated to RDA axes were plotted along with the ordination of sites and response variables. The relative position of the vector to each response variable or site in ordination space represents their correlation. Redundancy analysis was done with PC-ORD (Version 4.0, MjM Software, Gleneden Beach, OR, 1999).

We tested for a relationship between environmental variables and assemblage properties (assemblage similarity and P_i and P_e) using Pearson's correlation analysis. Because multiple comparisons were made among response and predictor variables, we used a procedure that reduces the probability of committing a Type I error while maintaining levels of power higher than those typical of traditional Bonferroni adjustments (Storey, 2002; Nakagawa, 2004). We controlled the expected proportion of false positives, or the false discovery rate (FDR; Benjamini and Hochberg, 1995; Storey, 2002; Verhoeven *et al.*, 2005). The FDR was estimated using the software package QVALUE Version 1.0 (Dabney and Storey, 2004, http://faculty.washington.edu /~jstorey/qvalue/) for R (Ihaka and Gentleman, 1996). The procedure generates q-values, which are interpreted in the same way as traditional p-values. We considered q-values ≤0.1 as significant.

We determined if less abundant species had higher P_e and if more abundant species had higher P_i. Both P_e and P_i were averaged across sites where the species was collected. On sampling events when the species was collected, abundance was averaged across sites and months to yield an average abundance of the species during the sampling period. We used linear regression to determine how much variance in P_i and P_e was explained by average abundance. The slope of each regression (m) was compared to the null hypothesis that it did not differ from zero. Abundance was square-root transformed prior to the analysis to help normalize the variance (McCune and Grace, 2002).

We determined if the stress of seasonal drought would adversely affect body condition for two common fish species. Condition was calculated following Love *et al.* (2005) and by estimating residuals from a linear regression on log-transformed mass by log-transformed length. The residual values were compared across months using ANOVA. Pairwise comparisons were made with a Tukey-Kramer's Post Hoc test. Regression and ANOVA were performed with SYSTAT (Version 10, SPSS Inc., Chicago, IL, 2000).

<center>Results</center>

<center>STUDY AREA</center>

The most dramatic environmental changes across sites over time were related to stream drying. Although spates in Jun. and Jul. re-connected five headwater pools periodically, pools were more isolated in Aug. and Sept., when the number of fish recaptures was much higher than Jun. and Jul. (ANOVA, $F_{1,54} = 6.43$, p = 0.01). These recaptures may be a result of pool drying or increased sampling efficiency of traps. Between Jun. and Sept., average pool size decreased 35% (repeated measures ANOVA, $F_{3,39} = 3.80$, p = 0.02) and the magnitude of change ranged from 13–100%, depending on pool location. Changes in pool size were greatest at upstream localities (Fig. 2A).

Dissolved oxygen, chlorophyll *a* and turbidity also showed high variability among sites. Dissolved oxygen values tended to be lowest at sites with high scores for distance, and that showed the greatest fluctuations in volume (Fig. 2A).

Fish assemblages.—We collected 544 fishes representing 18 species. An additional three species were observed, but not collected (*Etheostoma nigrum*, *Micropterus* spp., *Labidesthes*
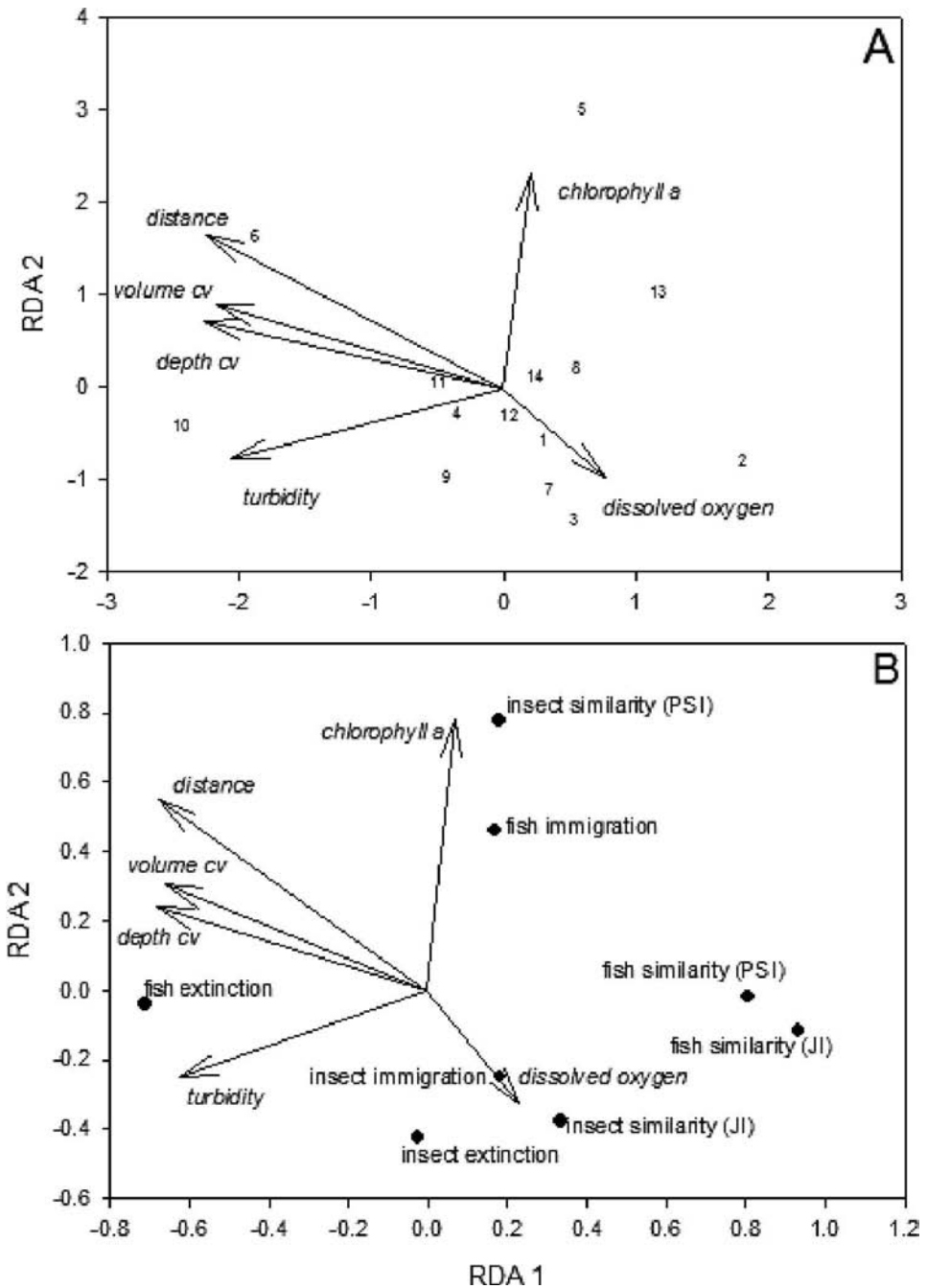
FIG. 2.—Redundancy analysis depicting the relationship between environmental variables and distribution of sites sampled in tributaries of the Alum Fork of the Saline River drainage (Jun.–Sept., 2002). (A) Displayed vectors represent the magnitude and direction of important habitat variables

Table 1.—Immigration (P_i) and extinction (P_e) rates for fishes averaged across sites (n) sampled in the Alum Fork of the Saline River drainage (central Arkansas, Jun.–Sept., 2002). We give relative abundance of a species for each month (JE = June, JY = July, AU = August, SE = September). CV = coefficient of variation in abundance for all sites and months. Species observed but not collected = —

Species	n	P_i	P_e	JE	JY	AU	SE	CV
Ameiurus natalis	3	0.61	0.33	0.0	1.2	1.5	3.0	1.2
Aphredoderus sayanus	10	0.46	0.25	11.0	15.3	12.7	8.0	0.1
Campostoma anomalum	10	0.56	0.73	0.0	5.9	0.7	9.0	1.4
Erimyzon oblongus	3	0.33	0.00	0.0	0.0	0.0	2.5	2.0
Esox americanus	3	0.44	0.66	0.0	0.0	0.8	0.5	1.2
Etheostoma artesiae	4	0.08	0.75	1.6	0.0	0.0	0.5	1.3
Etheostoma collettei	5	0.40	1.00	0.8	2.4	1.5	0.5	0.4
Etheostoma nigrum	2	0.50	1.00	—	—	—	—	—
Fundulus olivaceus	10	0.76	0.75	0.8	0.0	1.5	0.0	1.3
Hypentelium nigricans	1	0.00	1.00	0.8	0.0	0.0	0.0	2.0
Labidesthes sicculus	2	0.50	0.75	—	—	—	—	—
Lepomis cyanellus	13	0.66	0.36	65.8	36.5	46.3	48.0	0.4
Lepomis macrochirus	3	0.00	0.43	7.4	3.5	3.0	0.5	0.8
Lepomis megalotis	11	0.57	0.45	3.3	5.9	8.9	16.0	1.0
Lythrurus umbratilis	5	0.25	0.57	0.0	0.0	0.7	0.0	2.0
Micropterus spp.	4	0.56	0.63	—	—	—	—	—
Notropis boops	3	0.67	0.33	0.0	2.4	2.2	1.5	0.7
Noturus lachneri	8	0.44	0.37	3.3	7.1	11.2	4.5	0.6
Percina caprodes	2	0.50	0.50	0.0	2.4	0.0	0.0	2.0
Pimephales notatus	2	0.50	1.00	0.0	4.7	0.8	0.0	1.5
Semotilus atromaculatus	9	0.37	1.00	6.6	12.9	8.2	5.5	0.2

sicculus). *Lepomis cyanellus* (green sunfish) and *Aphredoderus sayanus* (pirate perch) dominated samples each month. *Lepomis cyanellus* were always abundant and occupied from 36% (Jul.) to 65% (Jun.) of the sample. Most of these were mainly juveniles (0.9 cm–8.0 cm, average = 4.63 ± 1.3 SD). Proportionately fewer *A. sayanus* were collected, ranging from 8% (Sept.) to 15% (Jul.). Individuals ranged in size from 3.0 cm–9.3 cm (average = 3.15 ± 0.8 SD). The relative abundances of the remaining 21 species occupied less than 10% of the sample. Relative abundance did not generally increase throughout summer (Table 1), suggesting that traps were not more efficiently collecting individuals as pools dried.

Fish assemblage properties were largely associated with physical habitat conditions and turbidity (Fig. 2, Tables 2, 3). Assemblages were most similar, on average, at downstream sites where habitat volume and depth were less variable and water clarity was higher (Table 2). Compositional changes in fish assemblages were mainly driven by P_e. Average P_e (0.56) was higher than average P_i (0.40) ($F_{1,26}$ = 5.93, p = 0.02), and was highest in upstream pools that varied greatly in volume and depth (Fig. 2).

Aquatic insect assemblages.—We collected a total of 3675 individuals representing 39 genera from Jul. to Sept. The Chironomidae and Heptageniidae (*Stenonema*) were the most abundant taxa collected at each site (Table 4). The Chironomidae increased in relative

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describing variation in environmental conditions across space and time. Each number represents a sampled site (*see* Fig. 1). (B) Environmental gradients related to assemblage properties for fishes and aquatic insects collected in tributaries. JI = Jaccard's Index of Similarity; PSI = Percent Similarity Index

TABLE 2.—Pearson correlations between assemblage properties and environmental variables in the Alum Fork of the Saline River drainage (central Arkansas, Jul.–Sept., 2002). Significance of the correlation was determined using the false discovery rate (FDR) procedure. Significant relationships (q ≤ 0.10) are in bold

	Fishes				Aquatic insects			
	P_i[1]	P_e[2]	PSI[3]	JI[4]	P_i	P_e	PSI	JI
Dissolved oxygen	0.09	−0.05	0.25	0.25	**0.70**	−0.04	−0.18	0.35
Dissolved oxygen CV	−0.30	0.29	−0.36	−0.28	**−0.55**	−0.26	0.29	−0.02
Depth	0.27	0.01	0.33	0.19	−0.47	−0.12	0.38	−0.35
Depth CV	0.14	0.46	**−0.66**	**−0.75**	0.05	−0.04	0.02	−0.50
Turbidity (log)	−0.16	**0.72**	−0.33	**−0.55**	−0.23	0.25	−0.30	−0.20
Chlorophyll *a* (log)	0.44	0.01	0.14	0.04	−0.30	−0.04	**0.64**	**−0.56**
Volume CV	0.05	**0.53**	**−0.61**	**−0.68**	0.08	0.00	0.20	−0.45
Volume	0.07	−0.12	**0.58**	0.47	−0.21	0.27	0.03	−0.05
Distance	0.25	0.46	**−0.62**	**−0.81**	−0.09	−0.44	0.19	−0.30

[1] Mean immigration rate

[2] Mean extinction (or emigration) rate

[3] Percent Similarity Index

[4] Jaccard's Index of Similarity

abundance from Jul. (49% of the sample) to Aug. (69% of the sample), but decreased slightly in Sept. (63% of the sample). Heptageniidae (*Stenonema*) became relatively less abundant from Jul. (45% of the sample) to Sept. (17% of the sample). In contrast, the relative abundance of Leptophelibiidae (*Paraleptophelibia*) increased from 0% in Jul. to 15% in Sept. All other genera occupied a lower percentage of the sample (<10%) (Table 4). Relative abundance did not generally increase throughout summer (Table 4), suggesting that traps were not more efficiently collecting individuals as pools dried.

Aquatic insect assemblage properties were primarily associated with DO and chlorophyll *a* concentration (Fig. 2, Tables 2, 3). These assemblages, on average, were most similar across summer in pools with high productivity or pools with high DO. Compositional changes were mainly associated with high P_i ($P_i = 0.44 > P_e = 0.34$, $F_{1,26} = 3.86$, $p = 0.06$), which was higher in pools with higher DO (Fig. 2; Table 3). Productive sites had similar assemblages over time (Table 2), possibly because of the domination by Chironomidae across sites (Table 4), but particularly at site five (Fig. 2) where they represented 98% of the entire summer sample.

Species properties.—At the species level, neither P_i nor P_e for fishes were associated with average abundance (P_i: n = 18, $r^2 = 0.09$, p = 0.23; P_e: n = 18, $r^2 = 0.05$, p = 0.37). For

TABLE 3.—Inter-set correlations of environmental variables with axes produced from a redundancy analysis on fish and macroinvertebrate data collected from the Alum Fork of the Saline River drainage (central Arkansas, Jul.–Sept., 2002)

Variable	Axis 1	Axis 2
Dissolved oxygen	0.2366	−0.2807
Depth (CV)	−0.6944	0.2024
Turbidity	−0.6371	−0.2144
Chlorophyll *a*	0.0701	0.6684
Volume (CV)	−0.6700	0.2598
Distance upstream	−0.6875	0.4734

TABLE 4.—Immigration (P_i) and extinction (P_e) rates for aquatic insect families averaged across sites (n) sampled in the Alum Fork of the Saline River drainage (central Arkansas, Jul.–Sept., 2002). Relative abundance (in percent) of each family given for each month (JY = July, AU = August, SE = September). CV = coefficient of variation in abundance for all months and sites. Data include samples from both Hester-Dendy plate samplers and D-frame sweep nets

Family (# genera)	n	P_i	P_e	JY	AU	SE	CV
Baetidae(1)	2	0.25	0.42	0.11	0.39	0.06	0.87
Caenidae(2)	5	0.38	0.50	0.00	0.59	0.17	0.64
Ceratopogonidae(1)	4	0.75	0.25	0.77	0.98	1.26	0.61
Chaoboridae(1)	1	0.50	0.33	0.00	0.00	0.11	1.73
Chironomidae(1)	14	—[a]	0.00	49.23	69.08	63.12	0.44
Coenagrionidae(1)	2	0.75	0.50	0.00	0.20	0.06	1.00
Cordulidae(3)	7	0.43	0.29	0.11	0.10	0.40	1.16
Culicidae(1)	1	0.25	0.50	0.00	0.00	0.17	1.73
Curculionidae(1)	1	0.00	1.00	0.11	0.00	0.00	1.73
Dytiscidae(1)	4	0.38	0.75	0.11	0.20	0.17	0.50
Elmidae(1)	2	0.75	0.50	0.00	0.20	0.06	1.00
Gerridae(2)	11	0.83	0.07	0.44	0.88	0.40	0.38
Gomphidae(1)	1	0.50	1.00	0.00	0.10	0.00	1.73
Gyrinidae(1)	5	0.80	0.06	0.11	0.39	0.11	0.66
Heptageniidae(2)	13	0.60	0.00	45.07	21.92	17.34	0.30
Heteroceridae(1)	1	0.00	1.00	0.11	0.00	0.00	1.73
Leptophlebiidae(2)	12	0.70	0.33	0.88	2.45	15.10	1.44
Libellulidae(3)	6	0.33	0.58	0.33	0.39	0.12	0.33
Nepidae(1)	1	0.50	1.00	0.00	0.10	0.00	1.73
Noctuidae(2)	2	0.50	1.00	0.67	0.00	0.20	1.73
Notonectidae(1)	4	0.50	0.33	1.54	0.00	0.69	0.87
Perlidae(1)	1	0.25	1.00	0.11	0.00	0.00	1.73
Polycentropidae(1)	3	1.00	1.00	0.00	0.29	0.00	1.73
Psephenidae(1)	1	1.00	1.00	0.11	0.00	0.17	1.15
Sialidae(1)	4	0.33	0.50	0.11	0.29	0.11	0.50
Siphlonuridae(1)	1	0.50	1.00	0.00	0.10	0.00	1.73
Veliidae(1)	3	0.33	0.33	0.11	0.00	0.11	1.00

[a] Taxon was always present and P_i was undefined

aquatic insects, P_i was also unrelated to abundance (n = 26, r^2 = 0.02, p = 0.47), but P_e significantly declined with increasing abundance (n = 27, r^2 = 0.30, p < 0.01). This latter relationship, however, was strongly driven by the Chironomidae, which were highly abundant and never went locally extinct.

Body condition for *Lepomis cyanellus* differed across months ($F_{3,257}$ = 11.56, p < 0.0001) and declined significantly between previous months and Sept. (Tukey-Kramer's test, p < 0.05; Fig. 3). In contrast, body condition did not change during summer for *Aphredoderus sayanus* ($F_{3,55}$ = 1.10, p = 0.36). These results are consistent with species-specific, local extinction rates; the P_e for *L. cyanellus* was nearly 1/3 higher than that for *A. sayanus* (Table 1).

DISCUSSION

Species responses to habitat fragmentation depend on habitat size (MacArthur and Wilson, 2001; Francour *et al.*, 2001; Oertli *et al.*, 2002), spatial configuration of habitats (Gergel and Turner, 2002) and quality of habitats (Pulliam, 1996; Donovan and Thompson,
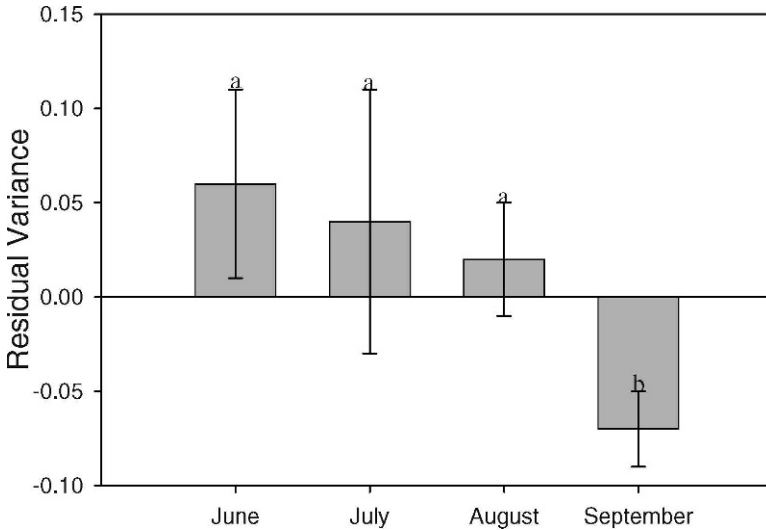
FIG. 3.—Monthly changes in body condition (residuals of length-mass regression relationship) of *Lepomis cyanellus* (green sunfish) collected in tributaries of the Alum Fork of the Saline River drainage (Jun.–Sept., 2002). Error bars are 95% confidence intervals of the mean. Superscript letters reflect significant differences (Tukey-Kramer's Post Hoc test)

2001). Seasonal fragmentation of intermittent streams and riffle drying during summer results in isolated pool communities (Magoulick and Kobza, 2004) that are strongly affected by physical factors that may differ in intensity across years (Dekar and Magoulick, 2007). Our results suggest that biotic responses (*i.e.*, immigration and extinction) to hydrologic and water quality conditions in streams during summer drought explain short term changes in community structure.

Assemblage variability for fishes was lowest in downstream pools that are typically larger (Taylor and Warren, 2001) and less hydrologically variable. Larger pools are more diverse (Angermeier and Schlosser, 1989; Taylor, 1997), which may be attributed to higher immigration and lower extinction than small or isolated habitats (MacArthur and Wilson, 2001; Taylor, 1997; Magnuson *et al.*, 1998; Taylor and Warren, 2001).

Declines in pool size influenced the extinction rates of fishes overall. Drying of isolated pools results in population declines of fishes (Lake, 2003; Magoulick and Kobza, 2003; Matthews and Marsh-Matthews, 2003) and local extinctions (Taylor and Warren, 2001), particularly for more isolated pools in upstream reaches. Declines in fish populations may result from higher predation rates by predators such as water snakes (Kofron, 1978), harsh physicochemical conditions (Magoulick and Kobza, 2003), emigration from degrading pools (Schaefer, 2001), density-dependent competition for resources, and a largely evaporated habitat. Species that are most influenced by factors such as competition or harsh physicochemical conditions may exhibit lower body condition, making them more susceptible to mortality (Love and Rees, 2002); in our study, body condition of *Lepomis cyanellus* declined through summer.

We found little relationship between abundance and immigration or extinction rates. These results differ from Taylor and Warren (2001) who found a positive relationship between abundance and immigration rates, and a negative relationship between abundance and extinction rates for this system at larger spatial and temporal scales. The differences in

patterns may have resulted from differences in sampling methodology (minnow trap versus electrofishing) and spatial scale. Taylor and Warren (2001) reported patterns across seasons and at the stream reach scale, while we studied intraseasonal patterns at a smaller spatial scale.

Aquatic insect assemblages changed little in pools that were eutrophying. These pools were consistently dominated by the Chironomidae. Low insect diversity in these pools may result from high fish density. High fish density may reduce pool quality for aquatic insects by inhibiting oviposition (*i.e.*, immigration; Resetarits, 2001), reducing aquatic insect densities (Williams *et al.*, 2003) and possibly increasing emigration rates (Love *et al.*, 2005). Biotic influences such as predation (Schlosser, 1987; Gilliam and Fraser, 2001), were not measured, but may have affected assemblage dynamics. Immigrants that may help maintain diversity may have been prevented from dispersal (via insect drift) because of riffle drying, or restricted oviposition. We found that habitats with high levels of DO had high rates of immigration during summer suggesting that aquatic insects may be selecting good quality habitat for oviposition. Pool-specific hypoxia may have also inhibited persistence of aquatic insect taxa. We did not estimate the size or distribution of terrestrial, adult populations, which may be more predictive of immigration rates than abundance of aquatic insect larvae during summer.

The often predictable interaction of environmental factors and dispersal (via immigration and emigration) on population structure suggests that a metapopulation approach may be useful for modeling population dynamics in intermittent landscapes (Gotelli and Taylor, 1999; Smithson and Johnson, 1999). Patches (*i.e.*, pools) in a metapopulation are characterized by immigration and extinction rates (Hanski and Gilpin, 1997) that differ predictably across the landscape (Taylor and Warren, 2001) as a function of habitat size (MacArthur and Wilson, 2001; Coleman *et al.*, 1982), habitat persistence (Taylor and Warren, 2001, this study), and habitat quality (Pulliam, 1996; Donovan and Thompson, 2001; Resetarits, 2001). In our study, multiple species disperse among pools, which may explain the persistence of local communities in upstream, harsh environments. Using the species-sorting, metacommunity framework of Liebold *et al.* (2004), we suggest that local communities undergoing desiccation are structured by predator-prey dynamics (Williams, 2003) and competition, and are maintained in harsh environments because of dispersal of many species into and from pool habitats.

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