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Influence of Fish Predation on Assemblage Structure of Macroinvertebrates in an Intermittent Stream

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Abstract.—Despite considerable investigation of stream systems, the influence of fish predation on macroinvertebrate assemblages is still poorly understood and remains a controversial subject. We conducted a field experiment in an intermittent reach of Alum Creek in the Ouachita Mountains, Arkansas, to examine the effects of predatory fish on macroinvertebrate assemblages. We tested the prediction that with pool isolation fish would have a top-down influence on macroinvertebrate assemblages. Overall, fish had a significant effect on both the density and assemblage structure of the macroinvertebrates in isolated stream pools. Assemblage effects may be linked to a feeding preference for relatively rare food items. These patterns were evident despite the loss of replicates (i.e., the drying of individual pools), indicating a strong short-term predator effect. We suggest that the use of different methodologies among studies makes it difficult to determine the influence of fish predation on macroinvertebrate assemblages in stream systems. Furthermore, we suggest that more realistic field experiments (i.e., with natural stream setting, hydrology, and substrata) must be conducted to fully understand and adequately address the question of the effects of fish predation on macroinvertebrates

One of the most important debates in the field of community ecology is whether ecosystem function is controlled by top-down or bottom-up trophic interactions (Matson and Hunter 1992). Much of the research in this area has been conducted in aquatic systems (Power 1992). In general, top-down trophic cascades are considered to be stronger in aquatic systems, particularly in simple, species-poor habitats (Strong 1992; Batzer 1998). These top-down effects have been well studied and effectively demonstrated for lentic systems (Carpenter et al. 198.5; McQueen et al. 1986; Scavia et al. 1986). Despite considerable investigation of lotic systems, however, the influence of fish predation on benthic macroinvertebrate assemblages is still poorly understood and remains a controversial subject. Allen (1951) found that trout in a New Zealand stream consumed from 40 to 150 times the estimate for macroinvertebrate production despite the fact that macroinvertebrates were common in drift. This pattern is known as Allen's Paradox. Since that time, a number of studies have found weak or no effects of fish predation (Allan 1982; Flecker and Allan 1984; Culp 1986; Reice 1991), while others have indicated strong effects (Flecker 1984; Gilliam et al. 1989; Schlosser and Ebel 1989; Power 1990).

Numerous hypotheses have been proposed to explain the lack of significant predator effects in lotic systems. These include immigration by macroinvertebrates (Flecker 1984), the presence of refugia and adaptations for predator avoidance (Allan 1982), alternative feeding on terrestrial food items by fish (Dahl 1998; Nakano et al. 1999), lack of competitive dominants (Allan 1982), and methodological differences among studies (Dahl 1998). Because low-order streams are less stable than lentic systems, disturbances to the former often have a stronger influence on community structure than biotic interactions (Menge and Sutherland 1987). Overall, the influence of predators on prey depends on the ecological characteristics of the organisms (e.g., assemblage structure and density of both fish and macroinvertebrates) and their environment

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(Power 1992; Pierce and Hinrichs 1997; Dahl and Greenberg 1998).

Intermittent streams provide an ideal system to examine factors influencing assemblage structure (Pires et al. 1999). When stream pools become isolated during dry periods, biotic interactions tend to be a more important regulator of assemblage structure than abiotic factors (Cowx et al. 1984; Dudgeon 1991; Flecker and Feifarek 1994). If flows provide connections among stream pools, the amount of refugia and number of microhabitats are increased and the influence of biotic interactions (i.e., predation and competition) is reduced (Hart and Merz 1998). As an individual stream pool begins to dry and becomes isolated, the abundances of organisms are controlled by a balance between predation and the increasing environmental harshness of the drying pool (Capone and Kushlan 1991).

We used an intermittent reach of Alum Creek in the Ouachita Mountains, Arkansas, to examine the effects of predatory fishes on macroinvertebrate assemblages in isolated pools. Small Ouachita Mountain streams have a highly variable flow regime over the year (Brown and Matthews 1995; Taylor 1997; Taylor and Warren 2001). Streams are maintained primarily by rainfall events; they are prone to flooding in the spring and to drying to isolated pools in the summer. Because the isolated pools represent sets of closed study units, they are an ideal system in which to conduct field experiments that examine the effects of biotic interactions on community properties. We predicted that when pools became isolated in Alum Creek, fish would have a top-down influence on macroinvertebrate assemblages. We were specifically interested in the effects of direct predation on macroinvertebrate assemblages. When stream pools are connected during wet periods, predators could presumably have both direct and indirect effects (e.g., inducing drift) on assemblages. Using isolated pools as the unit of study eliminated the concern about macroinvertebrate drift as a potential indirect effect. One limitation of most fish predation studies, at least from the standpoint of community ecology, is that only a single consumer is manipulated (Soluk 1993; Stelzer and Lamberti 1999). For this study, we examined the cumulative effects of the entire fish assemblage on their principal food source, the macroinvertebrate assemblage.

Study Area

The experiment was conducted in a single reach (about 150 m long) of a small (draining about 2,500 ha), second-order stream in the Ouachita National Forest (T2N R 19W S23; 34°48′53″N, 93°30′ 14″W). The Ouachita Mountains are a series of east-west ridges and valleys located in southeastern Oklahoma and southwestern Arkansas. Together with the Ozark Plateau, the Ouachita Mountains form the Interior Highlands Region of the United States (Robison 1986). The mountains are composed of Paleozoic sedimentary rock, and streams are dominated by bedrock, boulder, and cobble substrata with some finer sediments interspersed (Robison 1986). As there is little groundwater flow in these mountains, most of the smaller streams are maintained by rainfall events. The steep slopes of the region produce high-velocity floods in the spring, but most small streams dry to isolated pools by late summer (Taylor and Warren 2001).

Methods

Sampling methods.—During late spring (6 June) 1999, when Alum Creek was flowing, we identified 12 study pools to use in the experiment. After marking the pools, we set up a series of lateral transects, spaced at 2-m intervals, in each pool to measure stream environmental variables. Along each transect, we measured stream width and maximum depth. Depth and the dominant substratum were measured within a 0.25-m^2 area at four equidistant points along each transect (Taylor and Lienesch 1996). Substrata were classified as bedrock, large boulder (>300 mm in diameter), small boulder (150–300 mm), cobble (50–149 mm), gravel (3–49 mm), or sand/silt (<3 mm). Current velocity was measured with a digital meter (Marsh-McBirney Flo-Mate model 2000) at the thalweg along each transect. Cover variables (algae, emergent vegetation, and undercuts) were estimated as the percent area occupied along each transect. We used a concave spherical densiometer (Lemmon 1957) to estimate canopy cover at the center of each transect. In addition to the measurements taken along the transects, we measured the length of each pool and used the average length, width, and depth measurements to estimate pool volume.

After this initial effort, two pretreatment samples (20 June and 1 July 1999) were made while pools were still flowing. During each of these sampling periods, environmental data were collected as described previously, and benthic macroinvertebrates were collected with a vacuum benthos sampler (Brown et al. 1987) with mesh size of 600 μm (a mesh size that is appropriate for studies of the impacts of fish on macroinvertebrate assem-

TABLE 1.—Study design showing the allocation of treatments (removal of all fish or no removal [control]) to individual pools. The pools in the two groups differed in their environmental characteristics (see text). The groups were determined by means of a cluster analysis that used the average linkage method with 1 − the Pearson correlation coefficient as the distance metric. Only pools 1-5 were used in statistical analyses because the others dried up before posttreatment sampling was completed.

Pool	Group	Treatment
1	2	Control
2	1	Control
3	1	Removal
4	2	Control
5	2	Removal
6	2	Removal
7	1	Removal
8	1	Control
9	1	Removal
10	1	Control
11	2	Control
12	2	Removal

blages; A. V. Brown, University of Arkansas, personal communication). Two 5-min samples were taken at random locations within each of the 12 pools, and all macroinvertebrates collected were preserved for later identification.

We began the experiment on 29 July 1999, when we first noticed that flow between pools had ceased. The treatments consisted of (1) complete removal of fish from six pools and (2) no removal from six pools. We used the environmental data from 6 June 1999 in a cluster analysis (average linkage method with 1 − the Pearson correlation coefficient as the distance measure; Wilkinson et al. 1996) to group the pools based on environmental characteristics. The cluster analysis was successful in dividing the pools into two groups, and treatments were assigned randomly within these groups (Table 1). We used two groups to increase the replication of control and removal pools. The cluster analysis was used to reduce the probability that the results would be confounded by environmental differences among pools. Between the time that treatments were applied (29 July 1999) and the first posttreatment sample (6 August 1999), seven of the pools dried up (pools 6 through 12; Table 1; Figure 1). The remaining five (Figure 1) were sampled three times posttreatment (6, 15, and 21 August 1999). After the third sampling, three more pools became dry (Figure 1) and we ended the experiment.

We used backpack electroshocking (Smith-Root model 12-A) to remove fish from pools. After electroshocking, the pools were snorkeled to ensure that all fishes had been removed. Given the water clarity, small pool sizes, and low number of fish in these systems (Taylor et al., in press), we were confident of our ability to remove all fish. In addition, the pools were shocked during each posttreatment sample to ensure that they remained fishless. We removed the majority (56%) of fish on the first attempt and the remaining fish during the three subsequent posttreatment samples (7% on 6 August, 20% on 15 August, and 17% on 21 August). All control pools were also electroshocked to remove any confounding effects of this method on the macroinvertebrates. All fish in the control pools were returned to the stream alive. At each sampling period, the control pools were examined to ensure that they still retained appropriate numbers of fish. Fish removed from the removal pools were anesthetized and preserved for identification of gut contents.

Data treatment.—To characterize pretreatment environmental variability, a principal components analysis (PCA) was performed on the habitat data from the 6 June 1999 sampling period. We used the PCA to describe differences in stream habitat conditions between the two groups identified from the cluster analysis. We also used a multiresponse permutation procedure (MRPP; McCune and Mefford 1997), a nonparametric multivariate procedure that is functionally similar to a discriminant function analysis, on the habitat data to compare the two groups of pools.

We summarized the macroinvertebrate data within each pool for each sampling date. All macroinvertebrates collected were identified to family when possible. Because we were more interested in the functional response of macroinvertebrate assemblages than the responses of individual taxa, we did not identify organisms beyond family (see Bowman and Bailey 1997). Crayfish were excluded from all analyses because we could not accurately quantify them with our sampling methodology. We used a repeated-measures analysis of variance (ANOVA; Wilkinson et al. 1996) to examine the response of macroinvertebrates to fish removal over time. Specifically, we examined the effects on the mean taxa richness and density (per pool area) of macroinvertebrates. To examine the effects on overall macroinvertebrate assemblage structure, we performed a repeated-measures ANOVA on the mean scores along the first detrended correspondence analysis (DCA) axis. Detrended correspondence analysis is an ordination technique in which the scores along the axes represent a measure of turnover in species composition (beta di-

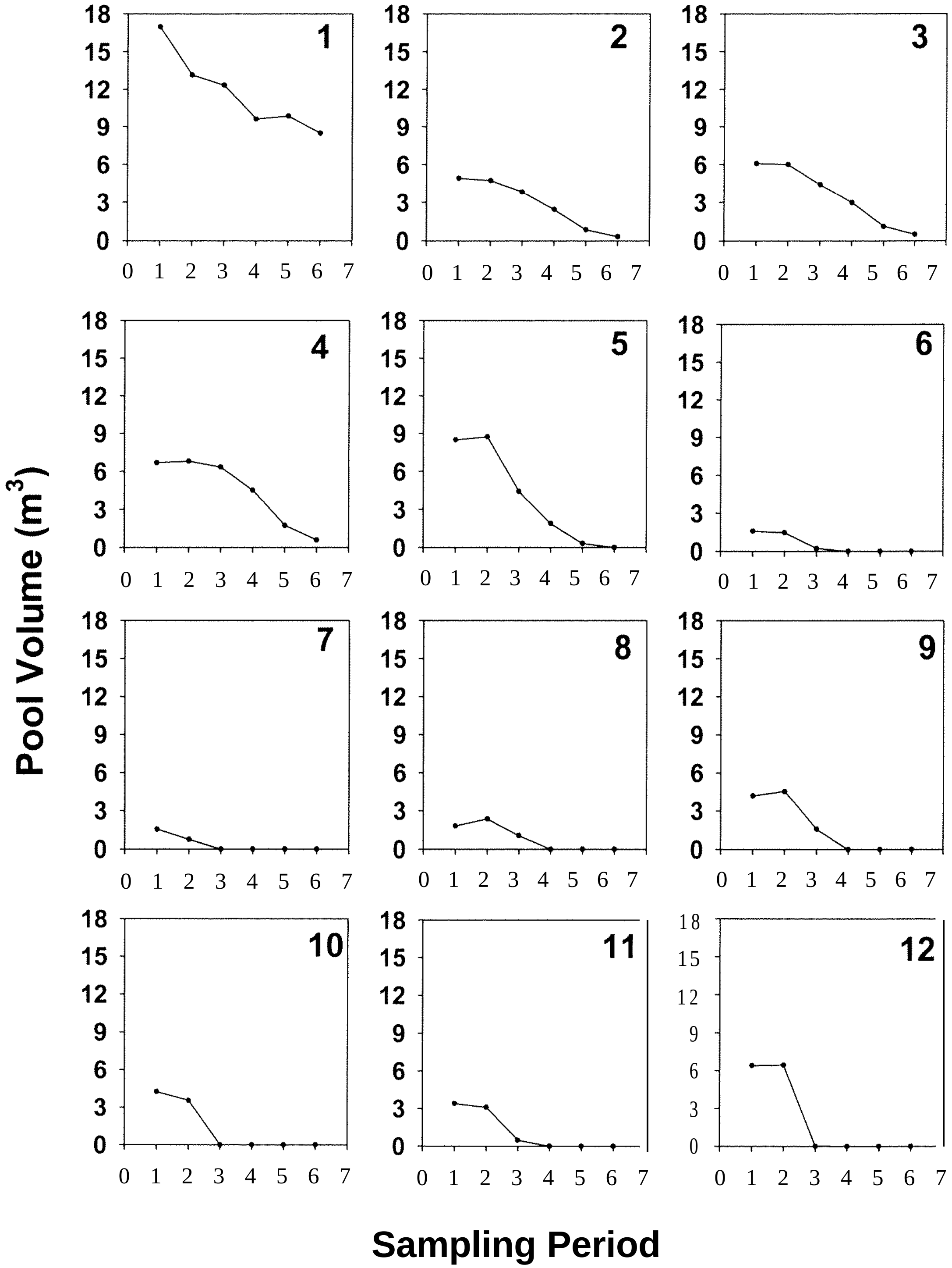

FIGURE 1.-Pool volume over time for all 12 study pools. Sampling periods 1 and 2 (20 June and 11 July 1999) were pretreatment, sampling periods 3-5 (6, 15, and 21 August 1999) posttreatment. Period 6 represents the conclusion of the study, when pools were too dry to collect more data. Only pools 1-5 retained water throughout posttreatment sampling.

versity) between sites (i.e., individual pools; Gauch 1982). For the purpose of this analysis, the first DCA axis represented shifts in the macroinvertebrate assemblages (or turnover in species composition) in response to the treatment. For the repeated-measures ANOVA, a significant treatment X time interaction would provide evidence of a response to the treatment. This would mean that there were significant shifts in macroinvertebrate density, richness, or assemblage structure over time because of the applied treatment. When the repeated-measures analysis produced a significant overall pattern, we tested the results from individual posttreatment sampling periods with a randomization test (sampling with replacement, 5,000 randomizations; Manly 1997). Randomization tests were used because of potential violations of parametric test assumptions.

Gut contents were examined and macroinvertebrates identilied for all fish removed from the pools. We removed the esophagus, stomach, and upper portion of the small intestine of each fish and extracted their contents. We identilied (usually to family) and counted all macroinvertebrates that were removed from guts. We used a linear index of food selection proposed by Strauss (I 979) to compare the proportion of each macroinvertebrate taxon collected from the field with the proportion removed from the guts of fish. This index has proven to be more robust than Ivlev's index of electivity or the forage ratio (Jacobs 1974; Strauss 1979). The values of this index range from 1 to − 1, with 1 being the strongest selection for a food item and − 1 indicating avoidance or inaccessibility. Values close to zero indicate random feeding by fish.

After the treatment effects were examined, we used MRPP to ensure that the response of macroinvertebrates was related to the treatment rather than to differences in stream habitat conditions among the pools. We sought to determine whether the removal pools differed in their habitat characteristics from the pools containing fish (control pools); the MRPP was carried out on the pre- and posttreatment habitat data separately.

Results

Pools in group 1 (Table I) were characterized by higher current velocity, higher percentages of cobble and small boulder substrata, higher percentages of emergent vegetation, less canopy cover, and greater length and surface area. In general. this group consisted of long, shallow. open pools. Pools in group 2 were characterized by greater volume, more boulders. more undercut banks, and greater canopy cover; these were deep, high-volume. shaded pools. Based on MRPP, environmental variation differed significantly ($P = 0.004$) between groups. By randomizing our treatments within these two groups, we reduced the possibility that environmental differences between the removal and control pools would contribute to differences in the response variables.

Overall, 70 individuals representing nine species (six families) of fish were removed from study pools (Table 2). Of these individuals, 40 had guts containing macroinvertebrates and 30 guts that did not. With the exception of central stonerollers and creek chubsuckers, all of these species were invertivores. Twenty-one of the 30 fish with "empty" guts were represented by these two species. Fourteen families of macroinvertebrates (10 orders) were collected from either individual pools or fish guts (Table 3). Two families of macroinvertebrates (Heptageniidae and Chironomidae) were numerically dominant in the collections and fish guts (Table 3). Heptageniids represented 82% of the organisms collected from the pools and 3 1 % of those found in the guts; chironomids made up 64% of the organisms removed from fish guts but only 5% of those collected from pools (Table 3). The value of Strauss's food selection index (Strauss 1979) for Chironomidae was high (0.585; Table 3), indicating strong selection. Selection for Heptageniidae, however, was relatively weak (-0.577; Table 3) despite their making up over 30% of the food items in the fish guts.

Fish removal had no effect on the taxa richness of macroinvertebrates (repeated-measures ANOVA, treatment X time; $F = 1.37$, df = 4, $P = 0.30$). There was, however, a strong effect on macroinvertebrate density over time (repeated-measures ANOVA, treatment X time; $F = 5.02$, df = 4, $P = 0.01$; Figure 2). Before treatment, removal pools had a slightly lower overall density, but there was a large increase in the density of macroinvertebrates after fish removal (Figure 2). By posttreatment sample 3, macroinvertebrate densities in removal pools were significantly higher than those in control pools ($P = 0.038$ for the randomization test).

Macroinvertebrate assemblage structure also showed a response to fish removal (Figure 3), although the interaction between treatment and time was not significant (repeated-measures ANOVA; $F = 2.12$, df = 4, $P = 0.14$). As a main effect, however, lime was significant (repeated-measures ANOVA; $F = 4.30$, df = 4, $P = 0.02$), indicating temporal shifts in the macroinvertebrate assem-

TABLE 2.—Number of individuals collected from removal pools (R; pooled across sampling periods) and examined for gut contents or electroshocked in control pools (C) and later released during the 29 July 1999 sampling period, by family and species.

Family and species	Pool number (treatment)				
	1 (C)	2 (C)	3 (R)	4 (C)	5 (R)
Cyprinidae					
Central stoneroller *Campostoma anomalum*	0	0	0	0	8
Bigeye shiner *Notropis boops*	0	1	0	0	0
Creek chub *Semotilus atromaculatus*	1	3	1	9	12
Catostomidae					
Creek chubsucker *Erimyzon oblongus*	4	5	2	5	11
Ictaluridae					
Ouachita madtom *Noturus lachneri*	2	1	0	0	7
Aphredoderidae					
Pirate perch *Aphredoderus sayanus*	0	0	2	0	2
Fundulidae					
Blackspotted topminnow *Fundulus olivaceus*	1	0	0	0	0
Centrarchidae					
Green sunfish *Lepomis cyanellus*	0	0	0	0	1
Longear sunfish *L. megalotis*	6	5	1	5	2
Percidae					
Creole darter *Etheostoma collettei*	2	1	0	0	19
Redfin darter *E. whipplei*	0	0	2	0	0

blages independent of treatment. The treatment effect was evident, however, when the individual posttreatment samples were examined with randomization tests (Figure 3). Although posttreatment sample 1 showed no significant response, samples 2 and 3 showed significant responses to fish removal (*P* = 0.04 and 0.03, respectively, for the randomization tests).

Before we could attribute the patterns described above to the treatment, we needed to show that the differences between removal and control pools were not caused by differences in the habitat conditions of the pools over time. The MRPP indicated that there was no significant difference in habitat conditions between removal and control pools, either pre- or posttreatment (*P* = 0.13 for both).

TABLE S.-Proportion of macroinvertebrate taxa in water samples and fish guts (I = 40) and value for Strauss's linear index of food selection (*L*). Data were pooled across sampling periods.

Order and family	Samples	Guts	*L*
Coleoptera			
Chrysomelidae	0.0007	0.0000	−0.0007
Dytiscidae	0.0013	0.0000	−0.0013
Elmidae	0.0007	0.0000	−0.0007
Gyrinidae	0.0280	0.0056	−0.0224
Copepoda	0.0000	0.0056	0.0056
Diptera			
Chironomidae	0.0530	0.6380	0.5850
Ephemeroptera			
Baetidae	0.0007	0.0056	0.0049
Caenidae	0.0007	0.0000	−0.0007
Heptageniidae	0.8220	0.3050	−0.5770
Leptophlebiidae	0.0065	0.0000	−0.0065
Hemiptera			
Corixidae	0.0104	0.0000	−0.0104
Gerridae	0.0250	0.0000	−0.0250
Isopoda			
Asellidae	0.0306	0.0056	−0.0250
Lepidoptera	0.0000	0.0056	0.0056
Odonata			
Corduliidae	0.0020	0.0056	0.0036
Oligochaeta	0.0039	0.0110	0.0071
Trichoptera			
Polycentropodidae	0.0059	0.0056	−0.0003

Discussion

In contrast to many previous studies (e.g., Allan 19X2; Flecker and Allan 1984; Culp 1986; Reice 1991), we Sound that fish predation had significant effects on macroinvertebrates. These effects were significant despite the uncontrolled presence of crayfish, another potential predator on macroinvertebrates (Charlebois and Lamberti 1996; Perry et al. 1997). Removing fish from individual stream pools led to a large and significant increase in the density of macroinvertebrates, a result also found by Flecker (1992a). The explosion in macroinvertebrate density (particularly in posttreatment sample 3; Figure 2) was primarily the response of heptageniids to the removal of fish. Even so, selection for this food item was not strong despite the fact that heptageniids made up a significant portion of fish diets. Fish may have been eating these mayfly larvae because they were so common in the environment rather than actively seeking them as a food source.

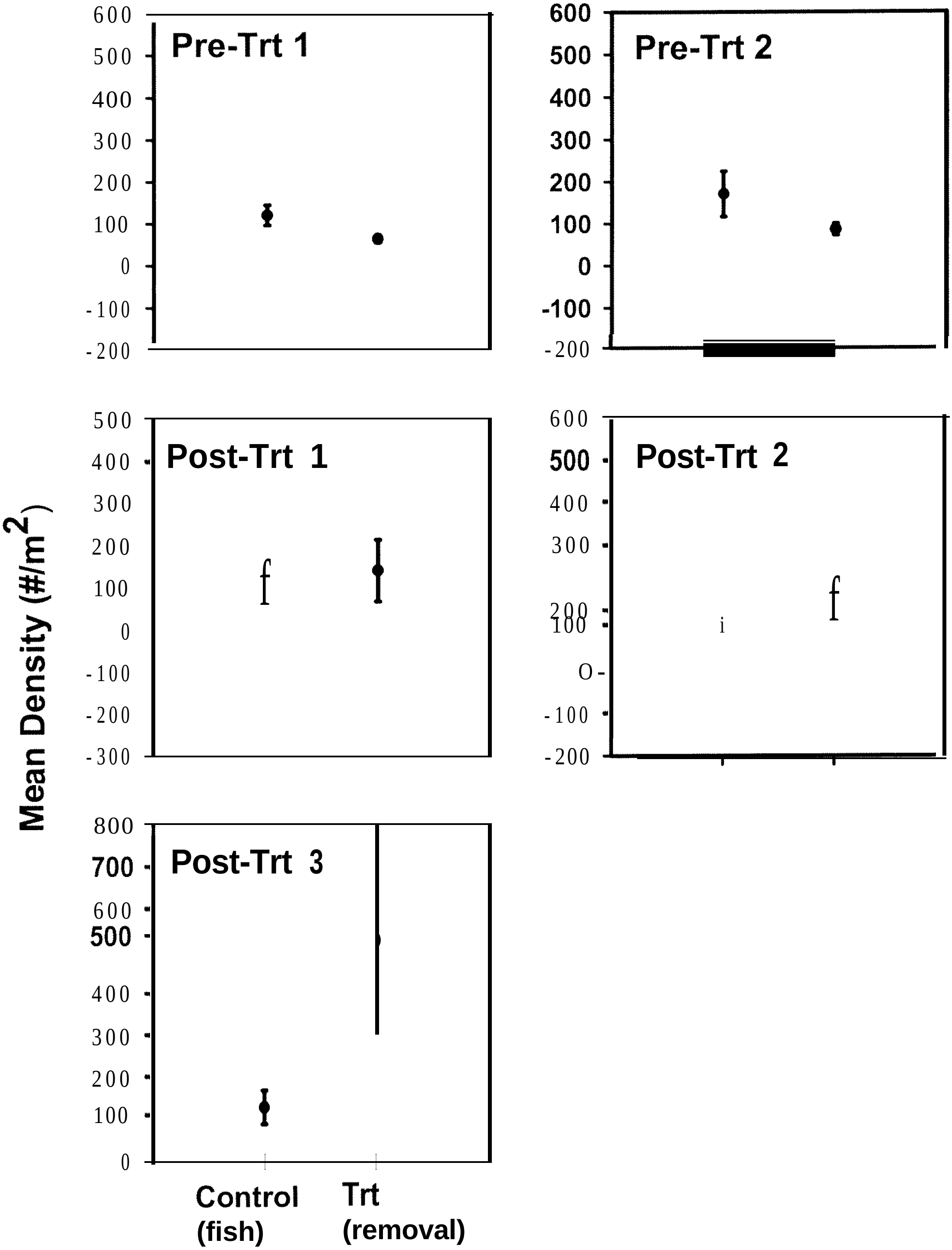

FIGURE 2.—Mean response of macroinvertebrate density per pool area to the fish removal treatment. Shown are means and SEs for the two pretreatment samples (Pre-Trt 1 and 2) and the three posttreatment samples (Post-Trt 1, 2, and 3).

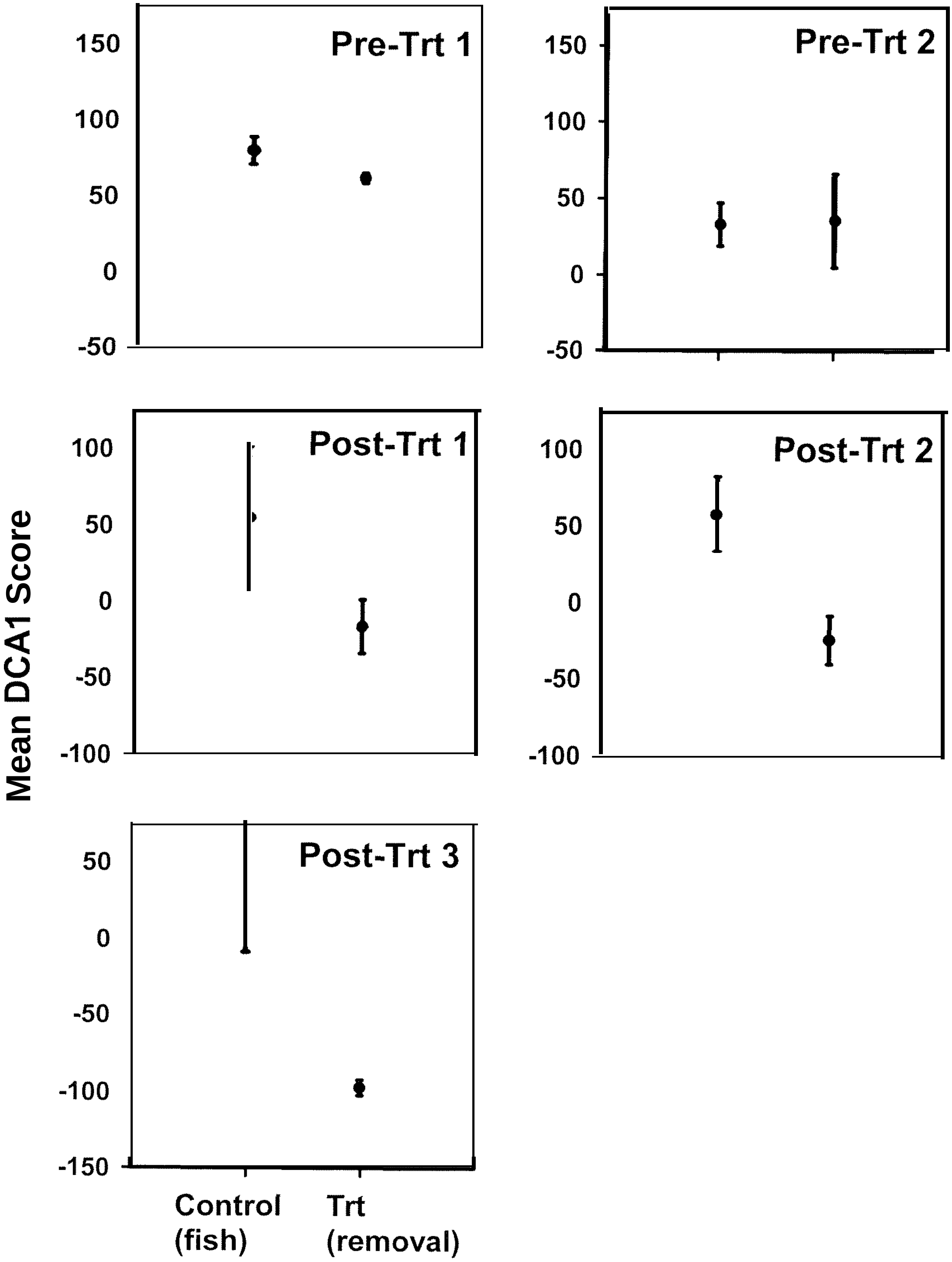

FIGURE 3.—Mean response of macroinvertebrate assemblage structure (represented by score along the first detrended correspondence analysis axis [DCA1]) to the fish removal treatment. Shown are means and SEs for the two pretreatment samples (Pre-Trt 1 and 2) and the three posttreatment samples (Post-Trt 1, 2, and 3).

We also found a significant predation effect on the assemblage structure of macroinvertebrates. Although macroinvertebrate assemblages showed significant shifts over time that were unrelated to treatments, mean response plots and randomization tests strongly suggest that fish removal affected the structure of these assemblages. One potential explanation is that the effect on assemblage structure was due to the selection of particular food items by fish. For example. chironomids seemed to be the most sought-after food item despite their relatively low numbers in the pools. An alternative explanation for the diet data (i.e., selection for chironomids and avoidance of heptageniids) is that our suction sampler differentially collected these families of macroinvertebrates. Chironomids may have been buried further in the substrate and thus more difficult to dislodge; however, during each 5-min sample we removed rocks, sifted through gravel and sand. and generally disturbed the substrate as deeply as we could penetrate. We felt we were collecting an adequate sample of the benthos because we were digging deeper into the substrate than were the fish. Further experiments would be needed to test the mechanism responsible for the macroinvertebrate density and assemblage structure effects.

In contrast to the above patterns, the taxa richness of macroinvertebrates was not affected by the treatment. Fish had an effect on the overall density or abundance of individual taxa without altering the absolute number of taxa. In other words, fish did not cause local extinction of individual taxa in the study pools, and there was no evidence that new taxa were invading or colonizing the pools over the course of the study. The fish fauna of the study pools was not particularly rich (i.e., few taxa and low abundances; Table 2). Streams in the upper Saline River basin, including Alum Creek, tend to have low species richness and abundances of fish (Taylor et al., in press). If fish had been more abundant, perhaps we would have seen stronger effects on macroinvertebrate assemblages.

Despite significant changes in stream habitat conditions over time, this environmental variability did not seem to override the effects of biotic interactions in the study pools (based on MRPP). This supports the idea that, at least for a period of time, biotic interactions may be a more important regulator of assemblage structure in stream pools than the environment (Cowx et al. 1984; Dudgeon 1991; Flecker and Feifarek 1994). In intermittent stream systems. biotic interactions may be the ultimate regulator of assemblage structure in the short term as individual pools become isolated from one another. Under such circumstances, individual pools become closed systems that do not allow macroinvertebrates the option of emigration by drift (Flecker 1992b) or other mechanisms that may ameliorate some of the effects of fish predation. If pools remain isolated for a long period of time and environmental conditions become severe (i.e., lead to physiological stress of the organisms), biotic interactions should become less important as the organisms struggle merely to survive the harsh abiotic conditions. Finding the critical point that balances the forces of predation and environmental variability will contribute greatly to our understanding of the ecology of small streams, but it will require a large, multiyear experiment beyond the scope of ours. Capone and Kushlan (1991) argued that environmental variability would be more important in regulating assemblage structure among pools while biotic interactions would be more important in regulating it within individual pools. We found that biotic interactions were an important regulator within stream pools, but individual pools did not remain isolated long enough for us to quantify the balance between risk of predation and the increasing environmental harshness of the drying pools (Capone and Kushlan 1991). Once pools became isolated in this experiment, they dried up very quickly. Within 1 week, a stream pool could go from being a functioning aquatic mesocosm to being completely dry (causing the death of all fish and likely of most macroinvertebrates as well). Because our posttreatment samples were 1 week apart, we were not able to catch the period of time right before pools became dry. A future study could narrow the temporal scale between samples to better understand how biotic interactions and abiotic harshness work together to structure isolated pool assemblages.

There are two primary advantages to this type of study as compared with many previous fish predation experiments. First, we examined the response of macroinvertebrates to the entire fish assemblage rather than to only one or two consumers. Second, the experiment was conducted in the field without enclosures or exclosures, using entire pools as experimental units. Thus. we were able to quantify assemblage-level changes within entire natural pool habitats. Because many stream-level processes are dependent on pool-level interactions, individual pools provide an excellent model system for ecological investigations (Matthews et al. 1994; Taylor 1997).

The major disadvantage to this type of field experiment is the difficulty of controlling the environmental conditions of stream pools. We lost 7 of 12 replicates because pools dried up before post-treatment data could be collected. We scouted the same pools in summer 1998 to assess their longevity, but 1998 was a wetter year in the Ouachita Mountains than 1999. Also, we could have increased the number of pools and spread them across an entire stream or several streams. Despite the potential confounding effect of this variability, we were able to determine that the patterns detected were related directly to fish predation and not to the environmental conditions of the pools. Although the power of our analyses was low because of loss of replicates, the patterns we found were statistically significant.

More-standardized field experiments in a variety of different systems should be attempted to understand fully the role of predation in stream ecosystems. To maintain a sense of reality in field experiments, we advocate taking advantage of natural fluctuations in hydrology whenever possible, rather than creating these conditions artificially. In our view, it was better to sacrifice statistical power (i.e., the potential loss of replicates due to pool drying) in order to account for the effects of natural variability on the system. In intermittent streams, individual pools essentially become isolated mesocosms that make ideal units for field experiments. Obviously, the conditions we encountered do not exist in every system, and thus our methodology cannot be applied to all stream systems. However, as long as inconsistencies in methodology (Dahl 1998) provide one of the most parsimonious explanations for the controversy about the effects of fish predation in stream systems, we cannot come close to understanding the role of predation in structuring aquatic ecosystems.

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References

Allan, J. D. 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. Ecology 63: 1444–1455.

Allen, K. R. 1951. The Horokiwi Stream: a study of a trout population. New Zealand Marine Department. Fisheries Bulletin 10, Wellington.

Batzer, D. P. 1998. Trophic interactions among detritus, benthic midges, and predatory fish in a freshwater marsh. Ecology 79: 1688–1698.

Bowman, M. F., and R. C. Bailey. 1997. Does taxonomic resolution affect the multivariate description of the structure of freshwater benthic macroinvertebrate communities? Canadian Journal of Fisheries and Aquatic Sciences 54: 1802–1807.

Brown, A. V., and W. J. Matthews. 1995. Stream ecosystems of the central United States. Pages 89–116 *in* C. E. Cushing, K. W. Cummins, and G. W. Minshall, editors. River and stream ecosystems. Elsevier, Amsterdam.

Brown, A. V., M. D. Schram, and P. P. Brussock. 1987. A vacuum benthos sampler suitable for diverse habitats. Hydrobiologia 153:241–247.

Capone, T. A., and J. A. Kushlan. 1991. Fish community structure in dry-season stream pools. Ecology 72: 983–992.

Carpenter, S. R., J. P. Kitchell, and J. R. Hodgson. 1985. Cascading tropic interactions and lake productivity. BioScience 35:634–639.

Charlebois, P. M., and G. A. Lamberti. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. Journal of the North American Benthological Society 15:551–563.

Cowx, I. G., W. O. Young, and J. M. Hellawell. 1984. The influence of drought on the fish and invertebrate populations of an upland stream in Wales. Freshwater Biology 14: 165–177.

Culp, J. M. 1986. Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry. Journal of the North American Benthological Society 5: 140–149.

Dahl, J. 1998. Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. Oecologia 116:426–432.

Dahl, J., and L. A. Greenberg. 1998. Effects of fish predation and habitat type on stream benthic communities. Hydrobiologia 361:67–76.

Dudgeon, D. 1991. An experimental study of the effects of predatory fish on macroinvertebrates in a Hong Kong stream. Freshwater Biology 25:321-330.

Flecker, A. S. 1984. The effect of predation and detritus on the structure of a stream insect community: a field test. Oecologia 64:300–305.

Flecker, A. S. 1992a. Fish trophic guilds and the structure of a tropical stream: weak direct vs. strong indirect effects. Ecology 73:927–940.

Flecker, A. S. 1992b. Fish predation and the evolution of invertebrate drift periodicity: evidence from neotropical streams. Ecology 73:438–448.

Flecker, A. S., and J. D. Allan. 1984. The importance of predation, substrate, and spatial refugia in determining lotic insect distributions. Oecologia 64: 306–313.

Flecker, A. S. and B. Feifarek. 1994. Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. Freshwater Biology 31: 131–142.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press. London.

Gilliam, J. F., D. F. Fraser, and A. M. Sabat. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. Ecology 70:445–452.

Hart, D. D., and R. A. Merz. 1998. Predator-prey interactions in a benthic stream community: a field test of flow-mediated refuges. Oecologia 114:X3-213.

Jacobs. J. 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413–417.

Lemmon, P. E. 1957. A new instrument for measuring forest overstory density. Journal of Forestry 55: 667–668.

Manly, B. F. J. 1997. Randomization, bootstrap, and Monte Carlo methods in biology, 2nd edition. Chapman and Hall. London.

Matson, I? A., and M. D. Hunter. 1992. The relative contributions of top-down and bottom-up forces in population and community ecology. Ecology 73: 723.

Matthews, W. J., B. C. Harvey, and M. E. Power. 1994. Spatial and temporal patterns in the fish assemblages of individual pools in a Midwestern stream (U.S.A.). Environmental Biology of Fishes 39:381–397.

McCune, B., and M. J. Mefford. 1997. PC-ORD: multivariate analysis of ecological data, version 3.0. MjM Software Design, Gleneden Beach. Oregon.

McQueen, D. J., J. R. Post, and E. L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 43:1571–1581.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stressand recruitment, American Naturalist 130:730–757.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial– aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441.

Perry, W. L.. D. M. Lodge. and G. A. Lambcrti. 1997. Impact of crayfish predation on exotic zebra mussels and native invertebrates in a lake-outlet stream. Canadian Journal of Fisheries and Aquatic Sciences 54: 120-I 25.

Pierce. C. L., and B. D. Hinrichs. 1997. Response of littoral invertebrates to reduction of fish density: simultaneous experiments in ponds with different fish assemblages. Freshwater Biology 37:397–408.

Pires. A. M., 1. G. Cowx, and M. M. Coelho. 1999. Seasonal changes in fish community structure of intermittent streams in the middle reaches of the Guadiana basin. Portugal. Journal of Fish Biology 54:235–249.

Power, M. E. 1990. Effects of fish in river food webs. Science 250:81 I-814.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy'! Ecology 73: 733–746.

Reice, S. R. 1991. Effects of detritus loading and fish predation on leafpack breakdown and benthic macroinvertebrates in a woodland stream. Journal of the North American Benthological Society 10:42–56.

Robison, H. W. 1986. Zoogeographic implications of the Mississippi River basin. Pages 267-286 *in* C. H. Hocutt and E. 0. Wiley, editors. The zoogeography of North American freshwater fishes. Wiley, New York.

Scavia, D., G. H. Fahnenstiel, M. S. Evans, D. J. Jude, and J. T. Lehman. 1986. Influence of salmonine predation and weather on the long-term water quality trends in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 43:435–443.

Schlosser, I. J., and K. K. Ebcl. 1989. Effects of flow regime and cyprinid predation on a headwater stream. Ecological Monographs 59:41–57.

Soluk. D. A. 1993. Multiple predator effects: predicting combined Functional response of stream fish and invertebrate predators. Ecology 74:219–225.

Stelzer, R. S., and G. A. Lamberti. 1999. Independent and interactive effects of crayfish and darters on a stream benthic community. Journal of the North American Benthological Society 18:524–532.

Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio. and a proposed linear index of food selection. Transactions of the American Fisheries Society 108:344–352.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73:747–754.

Taylor, C. M. 1997. Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. Oecologia 110:560–566.

Taylor, C. M., and P. W. Lienesch. 1996. Regional parapatry of the congeneric cyprinids *Lythrurus snelsoni* and *L. umbratilis*: species replacement along a complex environmental gradient. Copeia 1996:493–497.

Taylor, C. M., and M. L. Warren, Jr. 2001 Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. Ecology 82:2320–2330.

Taylor, C. M., L. R. Williams, R. A. Fiorillo, R. B. Thomas, and M. L. Warren, Jr. In press. Fish assemblage structure under variable environmental conditions in the Ouachita Mountains. *In* J. Guldin, editor. Symposium on ecosystem management research in the Ouachita and Ozark Mountains. U.S. Forest Service, Southern Research Station, Oxford, Mississippi.

Wilkinson, L., G. Blank, and C. Gruber. 1996. Desktop data analysis with SYSTAT. Prentice Hall, Upper Saddle River, New Jersey.