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Primary Research Paper

Impact of drought upon fish assemblage structure in two South Carolina Piedmont streams

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Abstract

The effects of drought on fish assemblages were studied in the Indian Creek (228 km^2) and Kings Creek (46 km^2) watersheds located in the Piedmont Province of South Carolina. Water and fish samples were collected at 13 localities during drought conditions in 2000 and again under post-drought conditions in 2003. Abundance, species richness, and Simpson's diversity were calculated for each locality, and the masses and lengths of individual fishes were measured to determine total biomass and length distributions for each species. Assemblages were significantly different from 2000 to 2003 at 10 of the 13 sample localities (χ^2 test for association; $p < 0.05$). The family Cyprinidae (minnows) was numerically dominant in both years and in both watersheds, but their dominance declined somewhat following the drought due to lower numbers of *Nocomis leptocephalus* and *Notropis lutipinnis* in 2003 collections. However, some cyprinids increased in abundance in 2003 collections, most notably *Semotilus atromaculatus* and *Hybopsis hypsinotus*. Abundance of catostomids (suckers) and ictalurids (catfish) was also decreased post drought. Conversely, centrarchids (sunfish) increased in dominance in 2003, especially the species *Lepomis macrochirus* and *Lepomis gulosus*. Many more juveniles and young of the year were observed in 2003 collections, suggesting that most species exhibited greater reproductive success following the drought. The significant differences in water chemistry observed between the two years were not associated with any change in fish community structure. Instead, we attributed the observed differences in fish assemblages to changes in habitat structure associated with higher rainfall during post-drought conditions. Finally, sample localities showed high variability in common measures of assemblage structure, including abundance, species richness, and diversity. We hypothesize that the observed variability in community structure is caused by the heterogeneous habitat structure and morphology of these small Piedmont Province streams.

Introduction

Unpredictable environmental disturbances commonly alter many aspects of stream systems, with variations in rainfall that affect stream discharge among the most important sources of natural disturbances (Taylor et al., 1996). Sudden or long-term variations in discharge, such as from extended droughts or large storms, can be particularly devastating, causing changes in water chemistry, stream size, water temperature, streambed structure, streambed substrate and stream flow (Medeiros & Maltchik, 2001). Such environmental variation can dramatically alter the living conditions and aquatic habitats within the water, affecting much of the aquatic fauna inhabiting streams (Moyle & Vondracek, 1985; Taylor & Warren, 2001).

Fishes are particularly susceptible to these changes in environmental conditions. Numerous studies have shown that changes in stream flow associated with extreme variations in precipitation can alter fish communities and habitats. Habitat structure is generally considered to be a good predictor of fish assemblage structure, so habitat instability associated with variations in stream flow will disturb the fish community residing within it (Meffe & Sheldon, 1990; Gelwick et al., 2001). For example, low discharge conditions during drought can limit habitat resources and fish mobility (Lohr & Fausch, 1997). Reproduction and juvenile recruitment can also be negatively affected by environmental stress associated with drought (Freeman et al., 1988; Schlosser et al., 2000). Commonly, drought simply kills fish directly (Lohr & Fausch, 1997). In contrast, high discharge associated with storm events can dramatically alter channel morphology and benthic habitat, which may have significant effects on fish communities. Many variables known to affect fish, including sediment load, pH, dissolved oxygen, and various nutrients, are frequently changed during increased flow associated with storm events (Winemiller et al., 2000; Ostrand & Wilde, 2002). Additionally, changes in discharge are known to cause changes in channel morphology (e.g., Leopold & Maddock, 1953), and variations in channel morphology are known to affect habitat and associated community structure (e.g., Frothingham et al., 2001). Extreme storm events that lead to flooding can introduce new species into assemblages and create new habitats (Meng et al., 1994; Winemiller et al., 2000).

Although variations in discharge have the potential to affect fish communities, the response of such communities to these changes is uncertain, particularly for longer-term drought cycles. Some studies have shown that diversity, species richness, abundance, and biomass are higher during droughts (Moyle & Vondracek, 1985; Grossman et al., 1998). Conversely, newer habitats could be created by higher water levels following floods, leading to increased species richness and diversity (Harell, 1978; Lohr & Fausch, 1997).

The purpose of this study was to compare the fish assemblage structure in drought and non-drought years in two small watersheds located in the lower South Carolina Piedmont Province (Fig. 1). In association with measures of fish assemblage we also compared discharge, stream depth and the chemical composition of the streams to assess changes in these parameters during drought and non-drought years. We hypothesized that changes in discharge leading to increased stream flow and water depth would alter both the physical habitat of the stream and its chemical composition, with these changes in turn influencing fish assemblage structure.

Methods

Study Area

Indian Creek (228 km^2) and Kings Creek (46 km^2) are small tributary watersheds near the mouth of the Enoree River in the Lower Broad River Basin of South Carolina (Fig. 1). The Enoree River watershed drains 1863 km^2 of the Piedmont Province in South Carolina. Both the tributary watersheds include a large area of the Sumter National Forest, which limits urban development. As a result, the land cover in the two watersheds is slightly greater than 90% forested (S. Muthukrishnan, personal communication).

All of South Carolina was considered to be in a "severe drought" from 1999 to April 2003 (SCDNR, 2003). Rainfall during the period of 1999–2001 was the lowest since the early 1950s. As a proxy for the effect of rainfall on stream discharge in the Indian Creek and Kings Creek watersheds, we use the discharge record of the nearby United States Geological Survey gaging station (02160700) located on the Enoree River in Whitmire, SC (Fig. 2). The hydrograph shows that during the summer of 2000, baseflow discharge was very low and storm flow events were small and infrequent. In contrast, during the summer of 2003, baseflow discharge was much higher with frequent storm flow events (USGS, 2003a). Although we do not have direct discharge measurements for localities in the Indian Creek and Kings Creek watersheds, the measured variations in discharge at the Whitmire gaging station are consistent with an increase in average stream depth from 2000 to 2003 in both the Indian Creek and Kings Creek watersheds.

Andersen et al. (2001) characterized the chemical composition of stream water in both

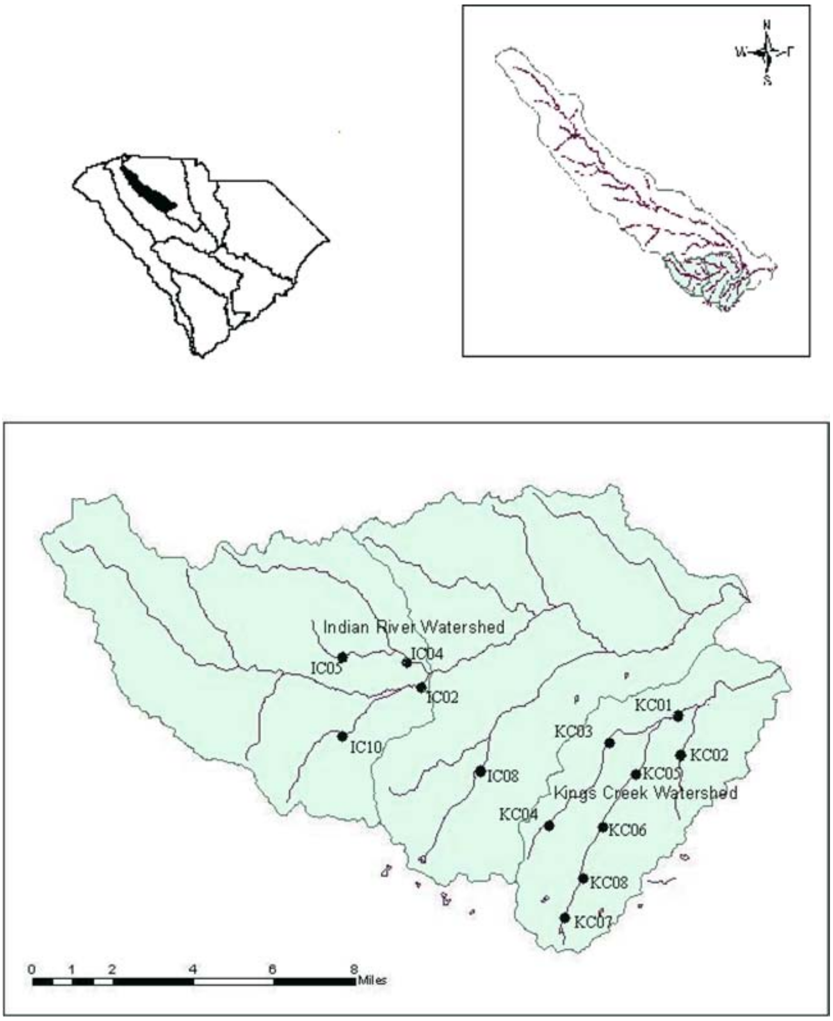

Figure 1. Map of the Enoree River watershed. Both Kings Creek and Indian Creek are small, southern tributaries of the Enoree River, which drains the piedmont of South Carolina. Individual sampling sites are shown.

watersheds during the drought period. Stream waters in both watersheds were dilute with low nutrient concentrations and moderate dissolved organic carbon concentrations. Nitrate concentrations averaged less than 1 mg/l, slightly higher than the average reported for undeveloped watersheds in the United States (Clark et al., 2001), but lower than more urbanized watersheds in the Enoree River basin, such as the Brushy Creek watershed (Gullikson et al., 2004). The results reflect chemical composition determined by bedrock weathering in a forested area and are characteristic of streams in the Piedmont Province of South Carolina and in other tropical to warm temperate regions (e.g., Edmund et al., 1995; Andersen et al., 2001; Andersen et al., 2004).

Fish collection and measurements

Sampling occurred in Indian Creek and Kings Creek from June through early August 2000 and again from June through July 2003. Sample localities chosen for study were those that could be sampled for fish during both low and high discharge. As a result, only five localities in the Indian Creek watershed and eight localities in the Kings Creek watershed could be sampled in both 2000 and 2003. At each site, fishes were stunned with a

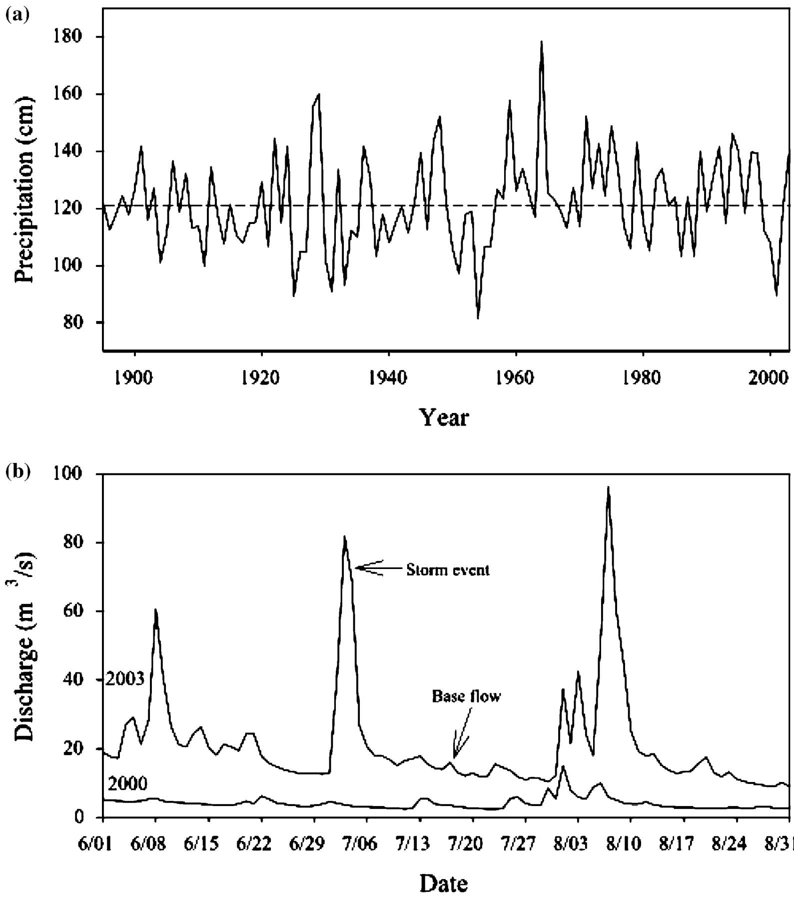

Figure 2. (A) Precipitation data for South Carolina from 1895 through 2003 (National Climatic Data Center 2004). The low rainfall in the late 1990s is equivalent to the drought in the 1950s. (B) Discharge values for the Enoree River at Whitmire, South Carolina from 1 June to 31 August for 2000 and 2003 (USGS 2003a).

Smith-Root Model 12-b POW backpack electrofisher set to 30 Hz and pulsed every 4 s for a total output of 400–700 V. Each site was sampled for a total of 480 s of electrofishing time to achieve an equivalent catch per unit effort (CPUE). Streams were sampled approximately 50–100 m upstream of the road crossing at each site, and every attempt was made to sample all available habitats. Fishes were collected using a 1/8″ × 4′ × 10′ seine and dip nets.

At the site, fishes were preserved using a 10% formalin solution. Samples were later transferred into 70% ethanol in the laboratory, then sorted and identified. Upon identification, standard length of each fish was measured with digital calipers (Fisher Scientific, Burlington, NC) to the nearest tenth of a millimeter. Excess alcohol was removed with a paper towel, and each fish was individually weighed with a digital balance to the nearest thousandth of a gram. All specimens are housed in either the ichthyology collection of the Florida Museum of Natural History in Gainesville, Florida, or in the department of Biology at Furman University in Greenville, South Carolina.

Water composition

Water samples were collected, processed, and analyzed following the methods of Andersen (2001) and Andersen et al. (2001). A total of six water samples were taken at each locality during summer 2000, whereas only one sample at each locality was taken prior to fish sampling in 2003. For comparison purposes, averages were used for the summer 2000 sample data. At each sample locality, conductivity, pH, dissolved oxygen, and water temperature were measured *in situ*. All water samples were analyzed for cation concentrations (Na^+, K^+, Ca^{2+}, Mg^{2+}, Si^{4+}), anion concentrations (F^-, Cl^-, Br^-, $H_2PO_4^-$, NO_2^-, NO_3^-, SO_4^{2-}), dissolved organic carbon (DOC), alkalinity, and turbidity.

Data analysis

For fish assemblage analysis at each sample locality for 2000 and 2003, abundance was calculated as the total number of fishes captured at each site during each sampling period, species richness was measured as the total number of different species captured at each site, and Simpson's diversity index was calculated as a weighted measure of diversity (Gurevitch et al., 2002). Total abundance, species richness, and Simpson's diversity data met assumptions of normality (Shapiro-Wilk W test; $p > 0.05$; JMP IN software, Version 5.1), therefore paired *t*-tests (Microsoft Excel Version 9.0) were performed to compare 2000 and 2003 samples at each locality. Abundance of selected numerically dominant species in each year was also compared. However, this data was not normally distributed, so the non-parametric Wilcoxon test was used for these comparisons (JMP IN software, Version 5.1). To compare community composition (the number of individuals of each species captured at each site) at each sample locality, a non-parametric χ^2 test for association (Microsoft Excel Version 9.0) was used to assess the degree of similarity between 2000 and 2003 samples. Significance for these and all subsequent statistical tests was considered to be $p \leq 0.05$.

For larger populations of individual fish species ($n > 10$ in each stream system per year), histograms were constructed to compare length distributions between 2000 and 2003. Data were not normally distributed, so the Wilcoxon test was used to compare overall lengths of fishes in these populations between the two sampling times (JMP IN software, Version 5.1).

The composition of water samples from 2000 to 2003 were compared using a χ^2 test for association (Microsoft Excel, version 9.0). Principal components analysis (PCA) was performed (MSVP, version 3.13b) using water composition data from all localities to assess the degree of similarity for the sites and the degree of similarity between 2000 and 2003. Principal coordinates analysis was performed (MSVP, version 3.13b) to test for multivariate relationships between fish community structure and chemical composition of the streams.

Results

Assemblage and population structure

Overall abundance in Kings Creek increased from 488 to 589 fishes captured from 2000 to 2003. Conversely, overall abundance of fishes in Indian Creek decreased from 599 to 555 (Fig. 3). In Indian Creek, the downstream sites (IC02 and IC04) had greater abundance in 2003, while the upstream sites all had lower abundance in 2003 than in 2000. Kings Creek, in contrast, had large variation from site to site. As in Indian Creek, the furthest downstream site (KC01) had greater fish abundance in 2003, but generally there was no predictable pattern observed. Abundance did not differ significantly in either Indian Creek or Kings Creek from 2000 to 2003 (paired *t*-test; $p > 0.05$).

Total species richness increased slightly, but not significantly (paired *t*-test; $p > 0.05$), in both the Indian Creek and Kings Creek watersheds from 2000 to 2003. Indian Creek increased from 15 total species captured in 2000 to 16 in 2003, while Kings Creek increased from 16 total species to 18. However, individual sites showed great variability, and no predictable trends for this measurement were observed (Fig. 3).

Generally, higher values for Simpson's diversity were seen at the sample localities closest to the confluence with the Enoree River (KC01, IC02; Fig. 3). Beyond this observation there was no predictable pattern in Simpson's diversity. There were no significant changes in diversity from drought conditions to post-drought conditions in either stream (paired *t*-tests; $p > 0.05$).

Species dominance results were similar for both Kings Creek and Indian Creek. Streams were dominated, both in terms of biomass and numbers captured, by cyprinids in both 2000 and 2003 (Tables 1 and 2; Fig. 4). Two species in particular, *Nocomis leptocephalus* (Girard) and *Notropis luti-*

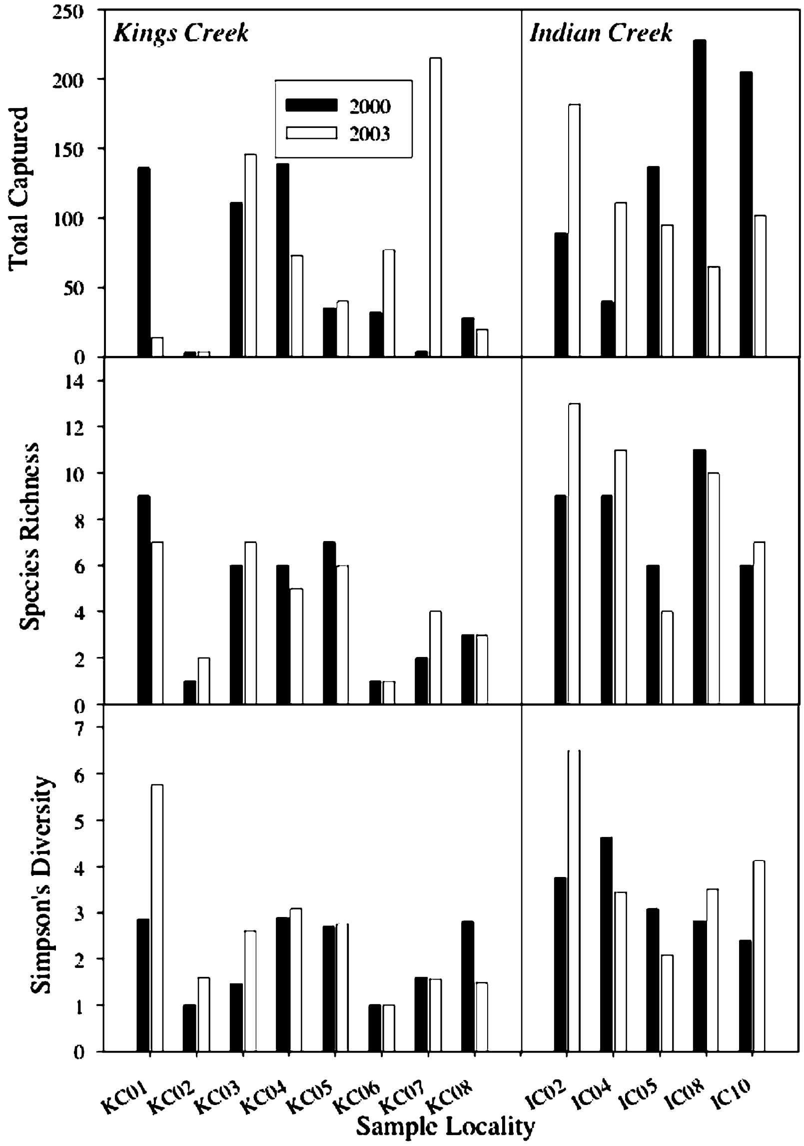

Figure 3. Abundance, species richness, and Simpson's diversity values for Kings Creek and Indian Creek in 2000 and 2003. Abundance is the total number of fishes captured at each sampling site, species richness is the total number of species captured at each sampling site, and Simpson's diversity is a weighted measure of diversity. Changes were not statistically significant (paired *t*-test; $p > 0.05$) for any parameter in either Kings Creek or Indian Creek.

pinnis (Jordan and Brayton), generally represented the greatest overall dominance in both watersheds and in both years. Biomass and numeric abundance values for these fishes decreased with greater discharge in 2003, although overall dominance of these two species remained high. The number of *N. leptocephalus* and *N. lutipinnis* captured at all sites in 2000 declined from 473 to 323 and from 310 to 140 individuals, respectively, in 2003. These declines in individuals, however, were not statistically significant because of high variability across localities. Several other cyprinid species increased in abundance and biomass values in 2003, including *Semotilus atromaculatus* (Mitchill) (increasing in number from 128 to 188) and *Hybopsis hypsinotus* (Cope) (increasing in number from 39 to 75), although again such increases were not statistically significant.

Table 1. Dominance values for all fish captured in Kings Creek in 2000 and 2003

Species	Family	2000 Numeric Dominance (%)	2000 Biomass Dominance (%)	2003 Numeric Dominance (%)	2003 Biomass Dominance (%)
Nocomis leptocephalus	Cyp	32.17	44.10	23.09	26.48
Notropis lutipinnis	Cyp	21.30	11.47	10.53	8.56
Gambusia holbrooki	Poe	20.69	3.92	29.03	12.85
Semotilus atromaculatus	Cyp	15.77	17.61	21.56	28.75
Etheostoma olmstedi	Per	4.50	1.70	0.34	0.32
Lepomis auritus	Cen	1.84	12.30	1.19	2.76
Ameiurus platycephalus	Ict	1.43	0.34	0	0
Esox americanus	Poe	0.82	4.57	0.17	0.52
Hybopsis hypsinotus	Cyp	0.41	0.29	3.56	3.67
Lepomis gibbosus	Cen	0.41	0.96	0	0
Lepomis macrochirus	Cen	0.21	0.57	3.06	7.32
Noturus insignis	Ict	0.21	0.55	0	0
Etheostoma thalassinum	Per	0.21	0.45	0	0
Etheostoma fusiforme	Per	0	0	4.58	2.23
Lepomis gulosus	Cen	0	0	1.12	2.91
Notropis scepticus	Cyp	0	0	0.68	1.22
Cyprinella nivea	Cyp	0	0	0.34	0.54
Hypentelium nigricans	Cat	0	0	0.34	0.95
Ameiurus natalis	Ict	0	0	0.17	0.58
Notemigonus crysoleucas	Cyp	0	0	0.17	0.36

Cyp = Cyprinidae, Cen = Centrarchidae, Cat = Catostomidae, Per = Percidae, Ict = Ictaluridae, Poe = Poeciliidae, Eso = Esocidae. Numeric dominance was calculated as number of fishes captured for individual species divided by total number of fishes captured. Biomass dominance was calculated as total mass of each individual species divided by total biomass of all fishes.

During 2003, there were increases in centrarchid dominance, especially in Indian Creek. The increase in centrarchid dominance at Kings Creek in 2003 can be attributed to significantly higher numbers of *Lepomis macrochirus* Rafinesque and *Lepomis gulosus* (Cuvier) in 2003 samples. Similarly, *Lepomis cyanellus* Rafinesque, *Lepomis auritus* (Linnaeus), and *L. macrochirus* each increased in number in Indian Creek in 2003, although increases were statistically significant only for *L. macrochirus* and *L. cyanellus*. Increases in abundance of these centrarchid species were also accompanied by increases in centrarchid biomass, particularly in Indian Creek.

Catostomids and ictalurids generally decreased in biomass and numeric abundance in each stream in 2003 compared to the low base flow period of 2000 (Fig. 4). However, numbers for both of these families were fairly low in both years. Poeciliids (*Gambusia holbrooki* Girard) exhibited very localized distributions, and were much more common in Kings Creek than Indian Creek. In Indian Creek, captures of *G. holbrooki* were rare. In contrast, in Kings Creek, *G. holbrooki* exhibited high biomass and numeric abundance in 2000 and 2003, increasing in both parameters in 2003. However, in both years captures of *G. holbrooki* were extremely localized, with all fish collected at just one site in 2003, and at just three sites in 2000, with one of these sites in 2000 comprising greater than 90% of all captures. In both years the high numbers of *G. holbrooki* captured was primarily due to the collection of a single large school of animals, resulting in the unusual observed distribution and dominance patterns.

Chi-squared analyses showed that the community composition found at 10 of the 13 sample localities from both watersheds changed significantly between 2000 and 2003. Sample localities that did not change were all in the Kings Creek watershed (KC04, KC06, and KC07). However, no consistent patterns in community composition

Table 2. Dominance values for all fish captured in Indian Creek in 2000 and 2003

Species	Family	2000 Numeric Dominance (%)	2000 Biomass Dominance (%)	2003 Numeric Dominance (%)	2003 Biomass Dominance (%)
Nocomis leptocephalus	Cyp.	45.20	33.70	33.60	23.0
Notropis lutipinnis	Cyp	28.10	12.40	14.10	4.80
Semotilus atromaculatus	Cyp	7.30	6.70	11.50	5.98
Hybopsis hypsinotus	Cyp	5.30	1.80	9.70	3.40
Hybognathus regius	Cyp	4.60	7.05	8.50	2.90
Lepomis auritus	Cen	3.00	8.80	4.90	12.60
Lepomis cyanellus	Cen	1.30	10.69	5.60	32.14
Notropis scepticus	Cyp	0.86	0.47	1.26	0.63
Erimyzon oblongus	Cat	0.86	4.54	0.90	2.77
Etheostoma olmstedi	Per	0.72	0.36	5.41	1.90
Ameiurus platycephalus	Ict	0.72	9.29	0	0
Noturus insignis	Ict	0.43	1.07	0	0
Gambusia holbrooki	Poe	0.43	0.009	0	0
Esox americanus	Eso	0.14	3.28	0.90	4.88
Scartomyzon rupiscartes	Cat	0.14	0.23	0.18	0.93
Lepomis macrochirus	Cen	0	0	2.30	3.20
Cyprinella nivea	Cyp	0	0	1.26	0.92
Hypentelium nigricans	Cat	0	0	0.36	0.68
Ameiurus natalis	Ict	0	0	0.18	1.85

Cyp = Cyprinidae, Cen = Centrarchidae, Cat = Catostomidae, Per = Percidae, Ict = Ictaluridae, Poe = Poeciliidae, Eso = Esocidae. Numeric dominance was calculated as number of fishes captured for individual species divided by total number of fishes captured. Biomass dominance was calculated as total mass of each individual species divided by total biomass of all fishes.

structure were seen either temporally or spatially in either watershed. Instead, we observed unpredictable variations from year to year and from site to site.

Size distribution

For most species, smaller fishes dominated the streams in 2003 compared to 2000. Although statistical comparisons were performed only on the dominant species (species with $n > 10$ in each stream system per year), with one exception, average size of all species captured in Kings or Indian Creek either did not change or declined in 2003. Size frequency histograms of the dominant species show that *N. leptocephalus, N. lutipinnis, L. auritus, and S. atromaculatus* were smaller in Kings Creek in 2003 when compared to 2000 collections, although the decrease was only statistically significant for *N. leptocephalus* and *S. atromaculatus* (Fig. 5). The only species whose average length was significantly larger post-drought were *G. holbrooki* captured in Kings Creek. Median size of all dominant species in Indian Creek decreased (Fig. 6). The cyprinids *N. leptocephalus, Hybognathus regius* Girard, *S. atromaculatus*, and *H. hypsinotus* all exhibited significant declines in median length. Of the dominant species, only *N. lutipinnis, L. cyanellus* and *L. auritus* were not significantly smaller post-drought. For many species in both streams, two or more distinct size classes were present in 2003, indicating that streams were populated mainly by young of the year and juveniles, with only some mature fishes.

Water chemistry

Precipitation in 2003 resulted in a significant increase in water depth compared to 2000 measurements in both the Indian and Kings Creek watersheds (paired t-tests, $p < 0.05$). On average, water depth increased about 55 cm at Indian Creek sample localities and about 45 cm at Kings

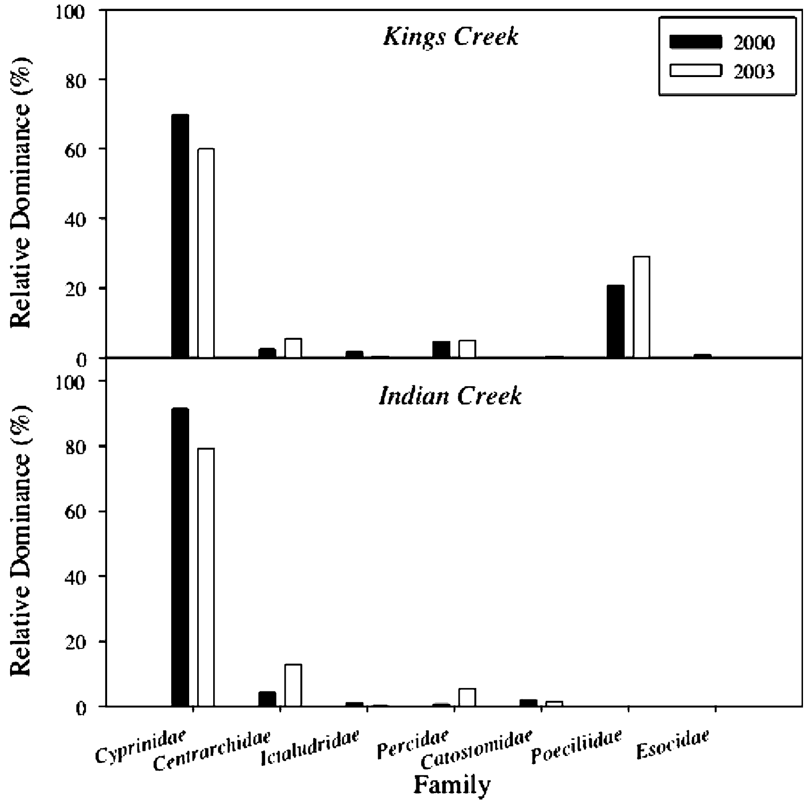

Figure 4. Relative dominance values for all families captured. Relative dominance is the total number of fishes of each family divided by the total number of all fishes.

Creek sample localities. Because these represent single measurements during base flow, the water depths represent only a gross estimate, but are indicative of the difference in hydrology between the two years. Data from the nearby U.S.G.S. gaging station indicates both an increase in base flow discharge and a greater frequency of storm events during 2003 (Fig. 2).

As expected with an increase in discharge, water samples from Indian Creek and Kings Creek watersheds differed significantly in water composition between 2000 and 2003 (χ^2 analysis, $p < 0.05$). In both watersheds, there were marked decreases in pH, conductivity, and concentrations of sodium, calcium, magnesium, and chloride in 2003. In contrast, the concentrations of sulfate, dissolved oxygen, and dissolved organic carbon (DOC) were higher in 2003. The PCA ordinates reflect this difference and clearly separate samples collected in 2000 from those collected in 2003 (Fig. 7). The data structure within each year, however, shows remarkable similarity, and indicates that the composition of Indian Creek samples was relatively distinct from Kings Creek samples.

No significant relationships between any single water chemistry measurement and any measurement of community composition were observed. Moreover, results of principal coordinates analysis did not indicate any multivariate relationships between water chemistry and fish community parameters.

Discussion

The effects of flooding and drought upon fish communities and assemblages have been studied extensively in many streams and under many conditions (Harrell, 1978; Ross & Baker, 1983; Bravo et al., 2001; Medeiros & Maltchik, 2001). Our data on fish assemblage changes, in combination with water chemistry data, hydrologic data, and size distribution information, allow for a more

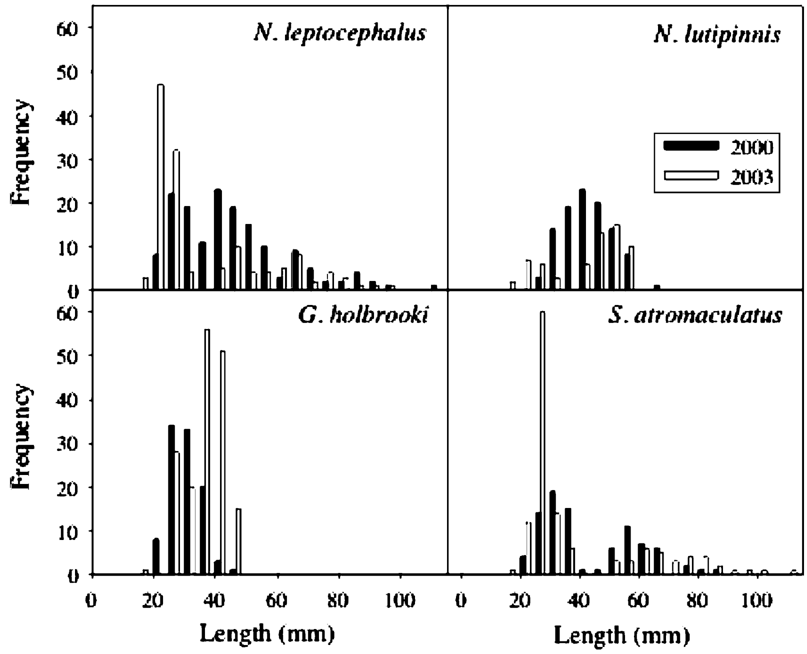

Figure 5. Size frequency histograms for fish species with large populations ($n > 10$) in the Kings Creek watershed in 2000 and 2003. All lengths are standard lengths. Median length decreased significantly (Wilcoxon test, $p < 0.05$) from 2000 to 2003 for *Nocomis leptocephalus* and *Semotilus atromaculatus*, but not for *Notropis lutipinnis*. Median length of Gambusia holbrooki increased significantly from 2000 to 2003.

comprehensive understanding of exactly how drought and post-drought environmental conditions affect fish communities in this part of the Enoree River drainage.

Water chemistry in both watersheds was significantly different in 2000 compared to 2003, with the observed changes in the composition of the stream water consistent with the increase in rainfall in 2003. The decrease in pH is directly attributable to the decrease in contact time of infiltrating water with soil and saprolite, and reflects the acidic rainfall observed in this area (USGS, 2003b). The increase in overland flow and surface runoff associated with the increased precipitation, as opposed to groundwater discharge, would lead to the observed declines in the concentrations of major cations and anions. Finally, we attribute the increase in sulfate to contributions of sulfuric acid in acid rain, and the observed increase in DOC and turbidity that is commonly associated with higher discharge. Our interpretation is based on interpretations of similar observed relationships between discharge and the concentration of DOC and sulfate in stream water (e.g., Lewis & Grant, 1979; Rice & Bricker, 1995).

Although the changes in water composition in the Kings and Indian Creek watersheds were significant and are consistent with increased precipitation, the chemical composition essentially changed from dilute to more dilute. The forested nature of the watersheds results in relatively pristine, dilute stream waters even during drought conditions (e.g., Andersen et al., 2001; Curry et al., 2001), so increased rainfall would result in increased overland flow and through flow and correspondingly more dilute stream water. The decrease in pH and conductivity and increases in sulfate and DOC, were statistically significant. Changes in chemical composition, however, were not statistically related to changes in fish assemblage structure. Therefore, the change in the chemical composition of the stream water does not appear to be environmentally significant.

Some previous studies have observed relationships between changes in water chemistry variables and fish assemblage structure. For example, Pinder & Morgan (1994) found that fishes, particularly cyprinid populations, are negatively affected by low pH levels. Winemiller et

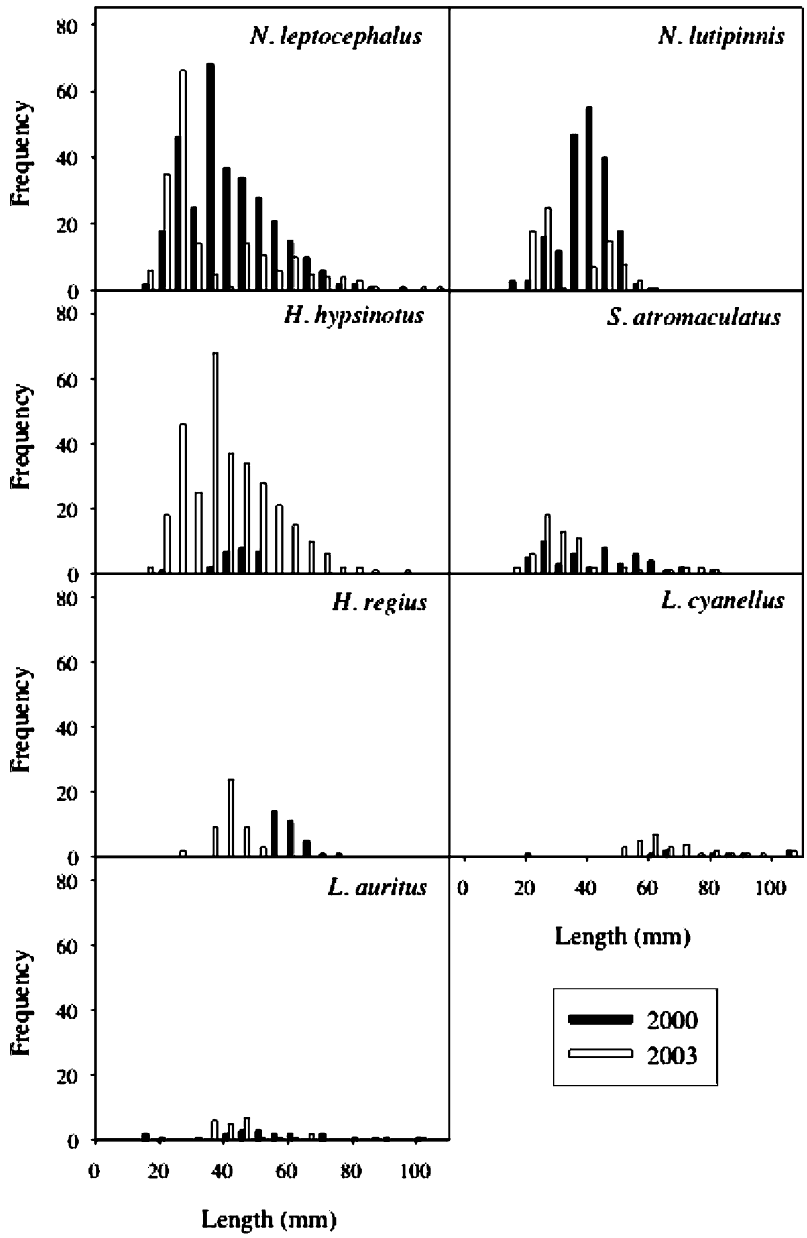

Figure 6. Size frequency histograms for fish species with large populations ($n > 10$) in Indian Creek watershed in 2000 and 2003. All lengths are standard lengths. Median length decreased significantly (Wilcoxon test, $p < 0.05$) from 2000 to 2003 for *Nocomis leptocephalus, Hybognathus regius*, *Hybopsis hypsinotus*, and *Semotilus atromaculatus*, but not for *Notropis lutipinnis, Lepomis auritus*, or *Lepomis cyanellus*.

al. (2000) showed that diversity and abundance of freshwater fish populations positively correlate with total dissolved nitrogen, nutrient concentration, and food resources in the water. Gelwick et al. (2001) found positive correlations between common measures of assemblage structure (diversity and abundance) and dissolved oxygen and salinity. However, while we observed significant changes in water chemistry, the degree of change in chemical composition we observed was minor compared to that reported in the studies cited above.

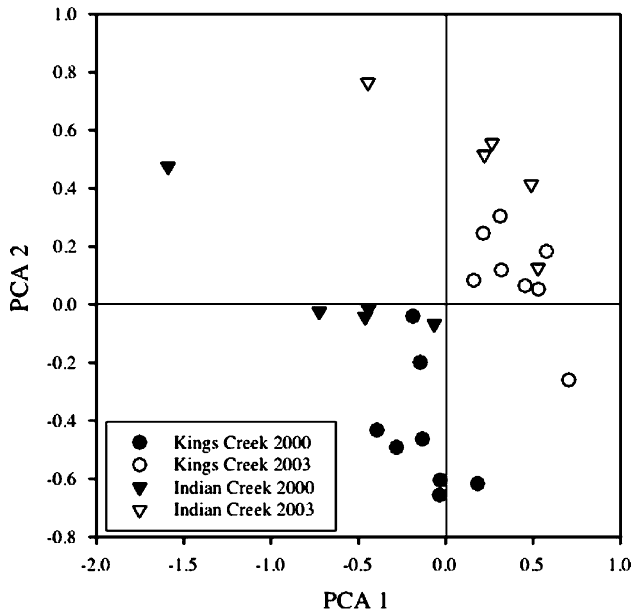

Figure 7. PCA scores for individual sites in Kings Creek and Indian Creek for 2000 and 2003. All units are in mg l^{-1} unless otherwise noted. Significant loadings onto PCA axis 1 were pH (−0.299), conductivity (μS cm^{-1}) (−0.357), Na^+ (−0.35), Ca^{2+} (−0.377), Mg^{2+} (−0.328), F^- (−0.369), and Cl^- (−0.311). Significant loadings onto PCA axis 2 were dissolved oxygen (0.293), dissolved organic carbon (0.418), K^+ (0.293), Si (−0.341), NO_3^- (−0.330), and SO_4^{2-} (0.378).

In contrast to the changes in water concentration, the greater than three-fold increase in depth for Indian Creek and two-fold increase in depth for Kings Creek have significant implications for the hydrology of the streams. Numerous studies have shown a direct relationship between an increase in depth and increases in stream width, stream discharge, and stream sediment load (e.g., Leopold & Maddock, 1953). Although we do not have other geomorphological data or direct discharge measurements, the combination of depth measurements, field observations, and data from the U.S.G.S. gaging station imply significant changes in the hydrology of the two watersheds. The combined effects of greater baseflow and more frequent storm events are consistent with a more dynamic habitat in 2003 than in 2000.

Because of this, we hypothesize that the community differences observed in both streams following the drought were caused by changes in habitat. Assemblage changes following a drought are frequently related to higher water levels in the stream system caused by increasing rainfall (Harell, 1978; Grossman et al., 1998), and physical changes to the stream and fish habitats often result from higher stream flow. These changes are considered to be key variables in shaping community structure. For example, increased water levels can affect streambed structure (Moyle & Vondracek, 1985), increase water depth (Harrell, 1978), and decrease the number of isolated pools (Gelwick, 1990). Freeman et al. (1988) found that such changes in local habitat structure contribute greatly to changes in fish population structure. Grossman et al. (1998) found similar results, arguing that changes in population structure following drought are due to shifts in habitat availability. Hatzenbeler et al. (2000) also attributed seasonal changes in abundance of fishes to changes in habitat. Finally, small streams, such as Kings Creek and Indian Creek, are highly susceptible to swift changes in habitat from flooding (Moyle & Vondracek, 1985). We conclude that changes in habitat availability were the most probable cause of shifts in fish communities in Indian Creek and Kings Creek from drought to post-drought conditions. Although changes in the numbers of individuals captured of each species in 2000 and 2003 were significantly different only for three species of centrarchids, the sum of these individual responses (both significant and non-significant) led to significant changes in community structure, as assessed by a χ^2 test for association, at 10 of 13 sample localities.

The family Cyprinidae is numerically dominant in both streams. While some species of cyprninds (most notably *S. atromaculatus* and *H. hypsinotus*) increased in dominance in 2003, the most abundant species decreased post-drought, and overall, cyprinid dominance declined 14% from 2000 to 2003. This decrease in dominance can largely be attributed to shifts in the two most abundant species: *Nocomis leptocephalus* and *Notropis lutipinnis*. These species were very abundant both years, but their numerical dominance declined by over 40% in 2003. Both species inhabit smaller rivers and streams, and usually occur further upstream in the headwaters (Jenkins & Burkhead, 1993). Meffe & Sheldon (1990) found that cyprinid populations are very mobile and responsive to changes in stream flow and changing stream conditions. It is possible that these two species moved upstream and to tributaries as water levels within the stream increased. Also, both *N. leptocephalus* and *N. lutipinnis* inhabit clear waters (Mettee et al., 1996), so the higher turbidities observed post-drought from rainfall and flooding could be detrimental to these species.

Another possible explanation for the smaller numbers of *N. leptocephalus* and *N. lutipinnis* is the increase in another cyprinid, *S. atromaculatus*. This fish is an aggressive piscivorous predator that can feed on small minnows (Mettee et al., 1996). Because *S. atromaculatus* is a larger fish associated with deeper pools, back waters, and slow runs (Jenkins & Burkhead, 1993), we hypothesize that the deeper water found post-drought created new habitat for this species, enabling it to increase in numbers and possibly feed on the other cyprinids. Others have observed this phenomenon, as Grossman et al. (1998) observed *S. atromaculatus* in most of their post-drought samples, indicating its ability to colonize and thrive in stream systems recovering from drought.

Like *S. atromaculatus*, other pool inhabitants exhibited increased populations in 2003. In particular, the family Centrarchidae showed greater abundance and biomass with the increased precipitation and stream water depths in 2003. Centrarchid numeric abundance increased two-fold in Kings Creek and three-fold in Indian Creek, with *L. macrochirus, L. gulosus*, and *L. cyanellus* significantly increasing in number from 2000 to 2003. Centrarchids are frequently found in pools and deep waters (Vadas & Orth, 2000) and were likely able to thrive in the deeper waters found during the greater water discharge in 2003. Magoulick (2000) also found that sunfish density is correlated to pool depth, so higher waters provide more habitat that allow fishes in this family to increase in number. Additionally, centrarchids inhabit areas with large amounts of woody debris (Quist & Guy, 2001). Habitat information recorded in 2003 from each of the sites shows logs, leaves, and tree limbs present at each site (unpublished data). We believe that storms caused much of this debris, providing cover and shelter for centrarchids.

The deeper waters promoting the centrarchid population increase were not beneficial to all families. For example, many species in the families Catostomidae and Ictaluridae decreased in dominance in 2003. Overall, catostomid and ictalurid numeric abundance declined 33% in Indian Creek and 68% in Kings Creek from 2000 to 2003. There are several possible reasons for this. Moyle & Vondracek (1985) found catostomids to be less abundant in the lower regions of their sample area with deeper waters. The absence of *Catostomus commersoni* (Lacepède), which normally lives in shallower streams and riffle areas (Jenkins & Burkhead, 1993), caused the reduced catostomid dominance in Indian Creek. A second reason for the change in both families can be explained by sampling difficulty. Catostomids and ictalurids primarily are benthic animals, living at the bottom of the stream in deeper areas that previous studies have shown to be more difficult to seine and sample by electrofishing (Jenkins & Burkhead, 1993; Vadas & Orth, 2000).

As noted above, drought and subsequent flooding affected individual species in Indian Creek and Kings Creek differently. However, most of the dominant species showed similar demographic trends. For most species, average size of all individuals was smaller in 2003, due in part to a higher proportion of juveniles and young of the year. The large number of smaller fishes presumably was a result of a greater reproductive success when water depths and discharge increased. Greater reproductive output is a common observation following a disturbance of any kind, as reproduction increases as the environment stabilizes (Meffe & Sheldon, 1990). Hot, dry drought conditions are known to kill younger fishes and decrease reproductive output in larger fish (Schlosser et al., 2000). Floods are favorable to reproduction and recruitment (Caltaneo et al., 2001), and thus higher water levels in 2003 likely alleviated stressful drought conditions and allowed for greater reproductive success.

Environmental stability could also be a potential explanation for the spatial trends observed in 2003. For example, downstream sites tended to be higher in abundance and diversity in 2003. Trends such as these are common (Moyle & Vondracek, 1985; Grossman et al., 1998) and are attributed to the stability of the environment. Grossman et al. (1998) found that the stream environment tended to be more stable in downstream sites and less susceptible to variation due to floods and drought. This environmental stability can potentially explain the higher abundance and diversity values seen in downstream sites in Indian Creek and Kings Creek.

Despite the general spatial trends observed, there was a large amount of heterogeneity among sampling sites. Although Kings Creek and Indian Creek are small streams, there were still a large number of differences between sampling sites and much variation in measures of assemblage structure. Streams often are described as heterogeneous and containing a complex mixture of habitats (Taylor and Warren, 2001; Ostrand & Wilde, 2002). Therefore, each site was likely affected by the drought and flooding in different ways, and local habitat variation may have influenced community structure in ways that precluded any observable trends in abundance, richness, or diversity.

Kings Creek and Indian Creek, like many stream systems, are greatly affected by environmental changes, and in these watersheds, changes in habitat associated with greater discharge and deeper water appear to be more important than water composition in affecting fish assemblage structure. This may be in large part because the watersheds are forested and thus the human impact on the chemical composition of the streams is relatively minor. As precipitation returns to normal levels in South Carolina, the streams may become less variable and more stable in the future. Additionally, the higher reproductive rates observed could have a large, long-term impact upon fish assemblages in these streams. Ongoing studies will be helpful to elucidate the long-term effects of changing water levels in these stream systems.

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