HABITAT CHARACTERISTICS AND FISH ASSEMBLAGE STRUCTURE OF DEEP POOLS IN THE UPPER TOMBIGBEE RIVER, MISSISSIPPI

By

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Fish assemblage structure in lotic environments is a product of interactions between the habitat and the biota, but little is known about how deep pool habitat conditions affect distributional patterns of fish occupying them in larger warmwater streams. This study describes relationships between the habitat and the fish assemblages in deep pools of the Upper Tombigbee River, Mississippi. Pools exhibited an increase in size from headwaters to mouth. The change in the structure of fish assemblages was related significantly to increases in pool size while independent of time or other environmental conditions. A small amount of the variation in structure of fish assemblages in deep pools was accounted for by the measured environmental variables. This suggests other factors such as biotic interactions play an additional role in the forming the observed distributional patterns in fishes occupying deep pools.

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CHAPTER I

INTRODUCTION

The structure and function of stream fish assemblages reflects the intricate connection between the habitat and the biota (Vannote et al. 1980). Fish assemblages in certain habitats are influenced by physical factors such as stream order (Gorman and Karr 1978; Peterson and Rabeni 2001), flow characteristics (Horwitz 1978; Meffe and Sheldon 1988), and depth (Angermeier 1987) that are typically within some tolerable or preferred range for a particular species. Biological factors such as food availability (Matthews et al. 1987) and predator avoidance (Fraser et al. 1987) also influence distributional patterns of fish and, thus, fish assemblages (Marsh-Matthews and Matthews 2000; Jackson et al. 2001).

Physical habitat factors, although often forming complex interactions to define the habitat, are relatively simple to measure and quantify; whereas quantifying biotic factors such as feeding selectivity and competition and, therefore, determining functional relationships among the biota and the environment, may be more difficult. Identifying relationships between physical habitat components and presence and abundances of fishes through preliminary observational studies should then be paramount in any study designed to investigate the ecology of a stream ecosystem or meet some management objective (Gorman and Karr 1978; Rabeni and Jacobson 1999). In addition, studies in

stream management and ecology often are designed to either estimate the population characteristics of a single species or make inferences regarding fish-habitat relationships for a few species. Describing the fish assemblage as a whole is not only easier to accomplish through sampling designs (Peterson and Rabeni 1995); but, when used with habitat data, provides essential information regarding what and why species may occur (Gorman and Karr 1978).

Riverine systems can be partitioned into a few major instream habitat types; ecologists and managers often segregate stream habitats by riffles and pools. Riffles are areas of shallow, swift water consisting of hard substrate, usually gravel and cobble, that provide habitats for fast–current-dwelling organisms. Because of the composition of the community occupying them, riffles function as feeding habitats for many species of fish (Thompson et al. 2001) as well as provide predator avoidance opportunities for smaller fish (Schaefer 2001). Pool habitats, defined by deeper depths relative to the entire river, provide another unique habitat to fish (Schlosser 1987; Capone and Kushlan 1991; Matthews et al. 1994b) due to their relatively stable habitat conditions over time. During periods of high stream discharge, some species may occupy pools because of the slower current velocities (Quist et al. 1999). In shallow cool- and coldwater rivers, high temperatures during summer may inhibit fish with low thermal tolerances from occupying shallow habitats forcing them to use these deeper habitats with cooler temperatures (Matthews et al. 1994a; Nielsen et al. 1994; Ebersole et al. 2003).

Although information about fish assemblage structure in riffles (Gelwick 1990) and in pools of streams where the depth typically does not exceed 2 m (Gelwick 1990;

Capone and Kushlan 1991; Matthews et al. 1994b) is available, little is known about deep pool habitat conditions and the distributional patterns of fish occupying them in larger warmwater streams (although see Lobb and Orth 1991). Because these habitats are for the most part non-wadeable, difficulties in sampling possibly has discouraged investigators. The lack of information regarding pool habitats and the fish assemblages occupying them not only limits our knowledge about structure and function of riverine systems, but systematically eliminating the sampling of difficult habitats may distort knowledge of habitat preferences and natural history (Aadland 1993). Of local interest in Mississippi, understanding the role of deep pool habitats in stream ecology may provide valuable information regarding habitat use of unique and imperiled species such as the Gulf Coast walleye *Sander vitreus* (Schramm and Miranda 2001) that may require habitat provided by deep pools in rivers and streams of northeast Mississippi (Schultz 1971; Kingery and Muncy 1990).

This study evaluates relationships between fish assemblages and habitat conditions in deep pools in the Upper Tombigbee River (UTR). The UTR provides a unique opportunity to investigate the ecology of warmwater lotic environments in that it has experienced little alteration. With its high turbidity, low stream gradient, and representative aquatic fauna, it is characteristic of most unaltered large warmwater streams in the United States (Rabeni and Jacobson 1999); thus, relationships established in this study may possibly be applicable to other warmwater streams. Few investigational studies have been presented in the published literature regarding the aquatic fauna and habitat characteristics of the UTR (although see Boschung 1987); therefore, an

opportunity exists to investigate ecological principles in a little-studied system and, at the same time, to provide information useful to conserve and manage non-wadeable warmwater streams in general. Specifically, the objectives of this study were to describe deep pool habitats, describe fish assemblages in deep pools, and determine if assemblage structure or individual species were associated with abiotic conditions within deep pools.

CHAPTER II

METHODS

Deep pools of the UTR were sampled monthly for one year to describe environmental conditions and fish assemblage structure. Principal components analysis was used to reduce the set of environmental variables down to linear combinations of variables that best represented the greatest sources of variation in habitat conditions in deep pools. Non-metric multidimensional scaling was used to provide a unique measure of fish assemblage structure in each pool. Using the results of the principal components analysis and non-metric multidimensional scaling, a multivariate analysis of covariance was used to evaluate differences in assemblage structure across sampling months and major environmental conditions within pools. Finally, canonical correspondence analysis was used to determine if environmental variables significantly accounted for patterns in fish assemblage structure and to assess specific species-environmental relationships.

Study Site

The UTR is a 3rd to 4th order stream in northeastern Mississippi. It originates near Marietta, Mississippi and flows with minimal instream alteration (except for a 2 km channelized stretch approximately 30 km from the headwaters) approximately 75 km

until it joins the Tennessee-Tombigbee Waterway (TTW) near Amory, Mississippi. The entire left bank riparian zone is state-owned land designated for wildlife and huntingmanagement. The river substrate is primarily sand with small gravel bars. The banks of the river average 1 m in height at average river stage, and the riparian zone is inundated at high flows. The river averages 5-m wide at the headwaters and 70-m near the confluence with the TTW. The riparian zone is forested lowland that contributes large woody materials to the river.

Selection of Study Pools

Deep pools were identified from bathymetric profiles of the river. Bathymetric maps were developed using a boat-mounted Lowrance® LCX-15 global positioning (GPS) and sonar unit. In fall, 2003, depth profiles were recorded by navigating at a constant slow speed along the thalweg of the river in upstream and downstream directions above and below each of three boat launching sites (referred to as reaches hereafter). The distance traveled in each direction was limited by shallow water and large woody material dams that prevented boat passage. The unit recorded an average of six depth measurements and one GPS location every second. These data were downloaded onto a computer and viewed using SonarViewer (Lowrance Electronics, Inc., Tulsa, Oklahoma). The GPS coordinate positions were converted to decimal degrees, and depths were converted to meters. This produced data points that were each associated with a latitude, longitude and depth.

Depths were recorded for each reach and standardized to the shallowest recorded depth for the specific reach where measurements were made. The data were then added as a point layer over a digital orthoquarter quad map of the river in ArcMap 8.3 (ESRI 2002). A color scheme was assigned to each depth percentile to facilitate interpretation. Pools for potential sampling were then chosen as those locations where depths were greater than or equal to the 90^{th} percentile depth for approximately 25 m or more of river length. Locations of these deep-water sites were transferred back to the GPS unit. I then returned to the locations of these pools and chose those sites that were accessible by the electrofishing boat (i.e., large woody material or other channel morphology did not prohibit access by the electrofishing gear). Sampling of any river is limited within the constraints of boat accessibility and navigation, and I distributed sampling as uniformly as possible. I chose 14 pools on the UTR as fixed sampling locations and numbered them from upstream to downstream (Table 1). Pools 1-5 were located at the most upstream portion of the river near Marietta, Mississippi. Pools 7-9 were in the mid-portion of the river near East Fork, Mississippi. Pools 10-15 were located in the lower portion of the river near Amory, Mississippi.

Fish Assemblage Sampling

Electrofishing is a widely used method of sampling stream fish, and recent equipment modifications have reduced sampling injury and mortality of fishes and improved the effectiveness in flowing waters with low conductivity (Reynolds 1996). Compared to other common sampling methods in lotic systems (e.g., hoopnets),

electrofishing has less variable catch rates and is less selective thus collecting a representative sample of the entire fish assemblage (Pugh and Schramm 1998). Fish were sampled using a boat-mounted Smith-Root® GPP 7.5 electrofishing unit. Because the conductivity of these rivers tends to be low (30-100 μS/cm), I used 1000 V output with alternating intervals of 15 Hz and 60 Hz pulsed direct current. In an effort to standardize electrical power output, conductivity (μS/cm) was measured before each sampling event and target power output of the electrofishing unit was calculated based on recommendations of Burkhardt and Gutreuter (1995). Catfish are common in these rivers and are better sampled with low frequency electrical current (Reynolds 1996), thus the inclusion of 15 Hz in my sample design. Each interval was approximately 30 seconds. Effort was applied until the entire area of the pool had been covered by the boat and no additional fish were seen surfacing. Equal effort was applied with each frequency at each pool with a minimum of 30 seconds of 15 Hz and 30 seconds of 60 Hz of shock time at each site. All fish collected were identified to species and released. Species abundances were expressed as fish/minute. Sampling was attempted at all pools monthly from March 2004 to March 2005. Due to safety concerns and in an effort to standardize sampling efficiency, I only attempted sampling when river stage was at low to moderate flow and had stabilized at this level for at least one week. I monitored river gauge height and discharge at the U.S. Geological Survey gaging station 02430500 in Marietta, Mississippi via real-time data available from the United States Geological Survey (http://water.usgs.gov/waterwatch).

Environmental Variables

Environmental variables were measured at each pool after fish were sampled. Depth (m) was recorded with the sonar unit to estimate the mean and maximum depth at each pool. Conductivity, which may affect the capture efficiency of the electrofishing gear (Reynolds 1996) and, thus, may be correlated with estimates of species abundances, was measured once at each pool with a YSI® Model 30 conductivity meter. Because conductivity is dependent largely on temperature, specific conductivity (i.e., conductivity standardized to 25C) was recorded. Canopy cover and large woody materials were subjectively measured once each sampling occasion by visual estimation of the percentage of canopy cover above the pool and the percentage of the pool area with visible large woody material.

Dissolved oxygen (mg/L), water temperature (C) and current velocity (m/sec) were measured at the surface, 40% of depth and bottom at a minimum of 4 and a maximum of 30 transects in each pool. Pool depth precluded use of conventional wadeable-stream habitat assessment methodology (c.f., McMahon et al. 1996; Barbour et al. 1999). Transects within a pool were made by anchoring at the upper end of the pool and drifting downstream, collecting measurements every 3 m. When the end of the pool was reached, the boat was anchored again at another haphazard location at the upstream portion of the pool and the process was repeated. Because current velocities within a pool can vary, current velocity measurements were replicated at each transect by taking measurements on the port and starboard sides of the boat. Mean current velocity for the

entire pool and coefficient of variation of current velocity (%) were calculated for each pool. The mean value for temperature and dissolved oxygen also were calculated. Dissolved oxygen and temperature were measured using a YSI® Model 550 dissolved oxygen meter. Current velocity was measured using a Marsh-McBirney Flow-Mate® Model 2000.

A bathymetric profile of each pool was made using the same procedure as used to survey for deep pools. This profile was created in ArcGis (ESRI 2002) and used to determine total area (m^2) and mean width (m) of each pool (Figure 1). Mean depth as mentioned above was used with the total area to calculate an approximate volume (m^3) for each pool on each sampling occasion. A 30-m resolution digital elevation model (DEM) of the river was used to approximate the elevations (m) of the surface of the pools.

Analysis

Detection of Sources of Variation in Deep Pool Habitat Conditions

Principal components analysis (PCA) was conducted using PC-ORD (McCune and Medford 1999) to reduce a matrix of sampling units and environmental variables by cross-products correlation into linear combinations of those variables that described the most variation in habitat conditions of deep pools. A sampling unit was a sample taken at a specific pool during a specific month. This method reduces the data matrix into a set of axes (or eigenvectors), each having an eigenvalue explaining the covariation of the

variables in the matrix (McCune and Grace 2002). Every variable then has a loading on each axis. The magnitude of the variable loadings indicate those variables that have the most influence on that axis, and the square of the loading is the percentage of variation in the variable explained by that axis (McGarigal et al. 2000).

Significant axes were determined as those with eigenvalues > 1. An eigenvalue > 1 ensures that the axis represents the variance of at least one variable in the data matrix (McGarigal et al. 2000). Axes, and thus the combinations of variables that explained the most variation in habitat conditions of deep pools, were defined by variables that had loadings greater than 0.32 and less than -0.32. This method is equivalent to choosing variables that account for at least 10% of the variance explained by that axis (Hair et al. 1987, cited in McGarigal et al. 2000).

I included thirteen variables in the PCA: mean depth, maximum depth, area, width, volume, elevation, mean dissolved oxygen, conductivity, mean temperature, mean current velocity, coefficient of variation of current velocity, percentage large woody material (LWM), and percentage canopy cover. All variables were log-transformed prior to analysis to comply with the linearity assumption of PCA except large woody material and canopy coverage, which were percentages and, thus, arcsine square-root transformed.

Fish Assemblage Structure

Often in community ecology investigations, species richness, Simpson's Index of diversity, or the Shannon-Wiener index are used as descriptors of assemblages (Marsh-Matthews and Matthews 2000; Gelwick et al. 2001). The dilemma with such indices is

the loss of the actual composition and relative abundance of the members of the assemblages. For example, the richness of one sample may be the same as another, yet their species compositions could be vastly different. If one were to use these descriptors, inferences could not be made regarding the changes in composition and relative abundance of multiple species in the fish assemblage. Therefore, a multivariate approach that considers species composition and relative abundance (hereafter, assemblage structure) can be useful. I calculated a multivariate measure of the fish composition and relative abundance in sampled assemblages of pools using non-metric multidimensional scaling, an ordination technique based on species abundances throughout the entire study. This method provides an interpretable measure of assemblage structure while preserving interrelationships between abundances of species within the assemblages.

Non-metric multidimensional scaling (NMS) is a non-parametric ordination technique used commonly to describe patterns in biotic communities (McCune and Grace 2002). Species abundances often do not exhibit linear trends across large environmental gradients but rather tend to follow a Gaussian (i.e., unimodal) distribution with zero occurrences at suboptimal environmental conditions. Non-metric multidimensional scaling assumes no underlying distribution and, thus, finds the best ordination solution regardless of the species response to environmental conditions. Because specific responses of the assemblages to environmental conditions in pools of the UTR are unknown, I chose to use NMS to estimate a measure of the structure of the sampled assemblages to ensure the ordination technique detected the actual structure of the assemblages rather than forcing the data to fit a specified model.

I used PC-ORD to conduct the NMS procedure based on a Bray-Curtis distance matrix of sample units and species abundances. All individuals captured at both electrofishing frequencies were combined for each sample unit. Species abundances were log(n+0.01). Log transformations are suitable when the variation of abundance data is high within species and within sample units (McCune and Grace 2002). The data were transformed because although NMS is a nonparametric procedure based on ranked distances, the Bray-Curtis distances are calculated from the original data that benefit from a linearization procedure. This will reduce any possible effects on the ordination solution of having a few species with low frequency of occurrence but high relative abundances. Because rare species can influence the final solution of the NMS procedure (McCune and Grace 2002), those species with relative abundances of less than 1% for the entire study were removed from analyses. The ordination scores for each sample unit on each of the significant axes were based on the abundances of the species in the data set. The species correlations with the detected axes give an indication as to those species that accounted for most of the variation in the assemblage data and thus had the greatest effect on the structure of deep pool assemblages. The unique combination of the ordination scores from each axis then provides a unique measure of the fish assemblage structure for each sample.

The final NMS ordination solution was determined using a procedure comparing solutions calculated with permutations of the actual and randomized data, therefore estimating significance values and ranges for stress values (McCune and Grace 2002). The stress of a solution is a measure of the departure of the ordination from the original

numerical structure of the data. For example, a stress value of 10% would be equivalent to the resulting ordination solution retaining 90% of the original variation in the data matrix. Using Kruskal's "rules of thumb" (Kruskal 1964, cited by McCune and Grace 2002) the ordination solution's ability to correctly represent the original variation contained in the data was considered reliable if the stress was less than 20%. A "good" final solution is described as a multidimensional ordination where the stress values have stabilized after 400 iterations of 40 permutations of the original data (i.e., the range of stress values for the multidimensional solution is relatively narrow). These stress values are considered significant if the proportion of stress values calculated from 50 random permutations of the original data that are less than or equal to the original stress of the original data is less than $\alpha = 0.05$. Percentage of variation explained by each axis was determined by calculating the correlation between the Bray-Curtis distances in original data and the Euclidian distances in the ordination results (McCune and Grace 2002).

Differences in Fish Assemblage Structure Across Time and Environmental Conditions

I conducted a multivariate analysis of covariance (MANCOVA) in SAS (SAS Institute 1985) to determine if the fish assemblage structure differed across successive sampling events or due to the environmental conditions most important in structuring pool habitat. In the model presented here, the response variables were the scores for each sample unit along all significant axes determined from the NMS procedure. Because multiple dependent variables were measured, the response variable in a MANCOVA is the centroid of the dependent variables measured on each sample unit. A centroid is a

multivariate mean or the center of a multidimensional distribution. The significant axes from the PCA results, representing combinations of multiple environmental variables that describe the most variation in habitat conditions of deep pools, were used as covariates in the MANCOVA. Sample units were grouped by month of sampling (the classification variable) to assess differences in the structure of the assemblages across successive sampling events.

The inventory of analytical methods available to assess differences in assemblages across space, time, or some other variable of interest is vast and ever growing. Univariate tests such as t-tests and analysis of variance have been used as basic methods to assess differences in species richness or diversity across sampling units and also have been used to partition the variation of some assemblage descriptor into spatial or temporal components (Lewis 1978; Matthews 1990; Meador and Matthews 1992). Subsequent multivariate techniques allowed visual interpretation of the dimensionality of species assemblage structure for time periods or geographic locations of interest (Robertson and Winemiller 2003). More complex models have been developed to combine multivariate ordination and univariate statistical tests to determine differences in individual axis scores due to time or some environmental variable (Gelwick 1990; Marsh-Matthews and Matthews 2000). These models require assignment of samples by *a priori* knowledge to fixed spatial locations, are vulnerable to violations of assumptions of the statistical tests used, and require multiple successive tests that may influence Type I error. The MANCOVA model allows detection of differences in assemblage structure across successive sampling events while simultaneously controlling for variation in the

assemblages due to linear combinations of variables that describe the greatest sources of variation in habitat conditions. Another appealing element of this model is that there is no assignment of samples to fixed classes therefore eliminating the use of subjective spatial classification in terms unsuitable for designs where the responses in assemblage structure are thought to be expressed along some continuum (e.g. Vannote et al. 1980). By condensing multiple univariate tests into one multivariate test, this model has the appeal of reducing the number of tests needed to come to a concise conclusion. In addition, outputs from most ordination techniques including NMS and PCA have been suggested (McCune and Grace 2002) as a method to linearize and otherwise meet assumptions of various statistical tests. Plots of all individual variables in the model (e.g., principal components axes) were evaluated for linearity. To ensure that I accomplished meeting some of the MANCOVA assumptions through ordination, SPSS (SPSS 1999) was used. Box's M test was used to evaluate homogeneity of covariances and Bartlett's test was used to evaluate sphericity.

Using the MANCOVA model, I first investigated temporal differences in the fish assemblage structure across the environmental covariates. This test determined if the response in the fish assemblage structure among pools to environmental conditions in pools differed across months. A significant interaction between a covariate and month would imply that the response in the structure of the fish assemblage to a specific covariate was different for each successive sampling event. If no interactions existed, I removed the interaction terms and used the model to determine if any environmental covariate had a significant effect on fish assemblage structure or if the fish assemblage

structure differed across months. A detection of a significant effect on the structure of the fish assemblage due to any one of the covariates would imply that the fish assemblage structure was related to the environmental condition(s) independent of the month of the sample. A significant month effect would indicate that the assemblage structure varied across time. All tests were considered significant at $\alpha = 0.05$.

Species Correlations with Environmental Variables

Canonical correspondence analysis (CCA) is a direct gradient analysis ordination technique designed to extract the most variation in a matrix of dependent variables that can be explained by a matrix of independent variables based on Chi-squared distances. For the purposes of this objective, PC-ORD was used to conduct CCA to extract major sources of variation in the abundances of species in the sampled assemblages that can be explained by the measured environmental variables within sampled pools. I considered the matrix of environmental variables from the PCA analysis as the explanatory matrix. The dependent matrix was the species matrix used for the NMS procedure.

Eigenvalues for the first three canonical axes determined by CCA were calculated and used to determine the percentage of the total variation in the species ordination explained by the ordination of the measured environmental variables along a particular axis. This percentage is calculated from the ratio of an axis' eigenvalue to the total variation in the species data that could potentially be explained by the environmental variables and allows inference about the relative contribution of the environmental variables in explaining the variation of species' abundances in the assemblages. A Monte Carlo procedure conducted with 999 randomizations was used to evaluate the

significance ($\alpha = 0.05$) of the eigenvalue for the first axis. Currently, there is a debate concerning the appropriate use of a Monte Carlo procedure to evaluate the statistical significance of any subsequent axes (McCune and Mefford 1999). This procedure was not available in the PC-ORD software and therefore was not attempted.

The CCA analysis produces descriptors that can be used to describe correlations between the species and environmental variables within the sampled assemblages. A correlation coefficient is calculated for each environmental variable along each axis and can be used to determine which variables are important in the overall ordination of species within environmental space. Environmental variables with correlation coefficients $-0.32 > r > 0.32$ along an axis were considered those correlated with that axis. In addition, for each axis, a percentage of variation in the species explained by the ordination is calculated as a ratio of the axis' eigenvalue to the total variation in the species data (McCune and Grace 2002).

In addition to calculating various correlation descriptors, CCA produces scores for species, sample units, and environmental variables that can be used to create graphs of the results known as biplots. Biplots facilitate visual inspection of the complex results of the CCA by indicating directional relationships between environmental variables and species abundances. The environmental variables are represented as vectors extending from the origin of the ordination of the environmental variables, and their lengths and direction indicate the correlation between the variable and that axis and with species in the sampled assemblages. In fact, the correlations mentioned in the paragraph above are the end-point coordinates for the environmental vectors. The proximity of environmental

vectors to one another represents correlations between environmental variables. Therefore, vectors extending in opposite directions represent inverse relationships between variables and vectors that extend in relatively the same direction represent variables that are positively correlated. When species are plotted with the environmental vectors, the strength of the relationship between a species' abundance and an environmental variable can be inferred by the placement of the species' plot relative to a vector. In addition, location of the species' points represents the optimal value of an environmental variable for that species within the measured data.

CHAPTER III

RESULTS

I collected 84 samples from the 14 pools during this study. Winter and early spring high discharges (Figure 2) and sampling equipment repairs constrained sampling and allowed sampling in most pools during only seven months: March, May, July, August, October, and November 2004 and March 2005. In four sample units I collected zero fish and two of only three threadfin shad *Dorosoma petenense* collected comprised the total catch in another sample unit. These five sample units were excluded from analyses. Four small cyprinid species were collected (in order of decreasing abundance): blacktail shiner *Cyprinella venusta*, Silvery minnow *Hybognathus* sp., Unknown shiner *Notropis* sp., and pretty shiner *Lythrurus bellus*. According to Ross (2001), these species often are found in open water habitat of large rivers in Mississippi, habitats similar to the pools in this study, and are thought to be habitat generalists. Because these four species require similar habitat and individually comprised a small portion of the total catch, they were combined into a single ecological-taxonomic group (minnow). A total of 465 fish from 25 species were collected in the remaining 79 sample units (Table 2). Species considered of special concern in Mississippi due to habitat loss and population declines (Ross 2001) were captured in this study: Chestnut lamprey *Ichthyomyzon cataneus*, and walleye. Fourteen species (including the minnow group) were prevalent in that at least

five individuals were collected among all sample units (Table 3). These 14 species varied in their abundance and frequency of occurrence across sample units.

Habitat metrics varied within and among deep pools (Table 1). Elevation varied from 88 to 55 m above sea level. Area varied from approximately 570 m^2 at the upstream-most pool to 12,700 m^2 at the pool farthest downstream. Pool width increased as elevation decreased. Mean depth increased longitudinally, and the range of mean depth within pools (i.e., the difference between the minimum and maximum mean depth measured in each pool) varied between 0.65 m and 1.91 m. Mean coverage of large woody material varied across pools but was less than 30% for all pools. Canopy coverage also differed across pools with a decrease in mean canopy coverage with an increase in pool area. Conductivity ranged between 39 and 222 μS/cm with greater mean conductivities occurring in the downstream pools. Greater conductivity values measured at pool 13 than other pools were attributed to the fact that this pool was located near the confluence of Town Creek with the UTR. Ranges for mean current velocity were greater in the upstream pools (1-5) and downstream pools (10-15). Mean temperature for all samples included in the analyses varied between 8.8 C and 31.0 C. Whereas mean temperature changed as expected with the seasons, the mean temperatures for the mid-reach pools were slightly warmer than those of the upstream and downstream pools across all samples. These spatial differences in temperature were negligible suggesting that though not all pools were sampled every month all pools were sampled across the entire range of temperatures experienced in the UTR. Mean dissolved oxygen

concentration varied between 3.6 and 9.7 mg/L with the least mean dissolved oxygen concentrations measured in the downstream pools.

Detection of Sources of Variation in Deep Pool Habitat Conditions

Principal components analysis of the 13 environmental variables measured for the 79 pool samples condensed the data into four significant (eigenvalue > 1) axes that explained approximately 81% of the total variation in habitat conditions of the sample units. The first principal axis (PC1) had an eigenvalue of 5.47 and explained 42.1% of the variation in the matrix of environmental variables measured on the sample units with area, width, and volume having large negative loadings ($r > -0.32$) (Table 4). Because of their interdependencies, together these variables are considered a descriptor of pool size. Elevation had a high positive loading on PC1 indicating an inverse relationship between pool size and the longitudinal position of the pool. Therefore, PC1 indicated a gradient in increasing pool size from upstream to downstream reaches and was the greatest source of variation in deep pool habitats.

The second principal axis (PC2) explained an additional 20.2% of variation in the environmental variables and had an eigenvalue of 2.63. Temperature and coefficient of variation in current velocity had high positive loadings on PC2, whereas mean current velocity had a high negative loading (Table 4). Therefore, PC2 described a relationship between current velocity descriptors and temperature for the sampled pools.

Axes three and four (PC3 and PC4) together explained an additional 18.6% variation in the environmental variables of the sampled pools and had eigenvalues of 1.28

and 1.15 respectively. For PC3, mean and maximum depth had high negative loadings whereas conductivity had a high positive loading (Table 4). Current velocity and dissolved oxygen had high loadings along PC4, but current velocity explained a larger proportion of the variation in PC2 and therefore was not considered in the interpretation of PC4. Thus, PC4 described the variation of dissolved oxygen concentrations in deep pools.

Plots of sample units along the first two significant axes demonstrate the ordination of sampled pools along the strongest detected linear combinations of variables representing habitat conditions. Upstream pools (pools 1-5) were typically smaller in size and are plotted to the far right on PC1, the area-width-volume axis (Figure 3). Downstream pools were larger and plotted to the far left on PC1. A plot of the two axes with sample units designated by sample month displays the change in current velocity with changes in temperature (Figure 4). Sample units in warmer months had slower current velocities and were plotted higher on PC2, the temperature-velocity axis. Although temperature and current velocity varied with time, this variation was consistent across all pools; the lack of vertical spread in sample units plotted by month of sample indicates that pools sampled in the same month had relatively similar temperature and current velocity measurements. These results suggest a high degree of variation in abiotic conditions of sampled pools that may potentially affect fish assemblages.

Fish Assemblage Structure

Based on the permutations of the original and randomized data, the fish abundance data for the 14 most abundant species in the 79 sample units were best described by a three dimensional solution. The stress of the final three-dimensional solution was 17.6%, indicating that the reliability of the ordination was sufficient in retaining the original structure of the entire matrix of species by sample units. The ranges for the calculated stress values of the three-dimensional ordination were smaller relative to the other dimensional solutions and the randomized stress value was statistically significant (Table 5). The three axes explained approximately 76% of the total variation in the species assemblage data. Flathead catfish *Pylodictis olivaris* and longnose gar *Lepisosteus osseus* had strong correlations with axis 1 (r = -0.69 and -0.60 respectively, Table 6). Freshwater drum *Aplodinotus grunniens* had the highest correlation with axis 2 (r = -0.44). Smallmouth buffalo *Ictiobus bubalus* and the minnow group had the highest correlations with axis 3 (r = -0.70 and 0.57 respectively). Thus the structure of the species assemblages of the sample units was influenced strongly by the occurrences and abundances of these five species.

A plot of sample units coded by pool along the first two axes calculated by NMS displayed some segregation among assemblages in different pools (Figure 5). A plot of sample units coded by month of sample along the first two axes calculated by NMS displayed poor segregation among assemblages sampled across time (Figure 6). These plots did not visually provide strong evidence of temporal differences in assemblages but may hint at some spatial arrangement of pool assemblages.

Differences in Fish Assemblage Structure Across Time and Environmental Conditions

The four significant axes from the PCA procedure were used as covariates in the MANCOVA model. The first covariate was described as an increase in pool size along an elevation gradient (PC1). The second covariate was a combination of current velocity, variation in current velocity, and temperature (PC2). The third covariate was a combination of conductivity and mean and maximum depth of the pools (PC3). The fourth covariate described variation in dissolved oxygen (PC4).

The data met all assumptions necessary for the MANCOVA design. No significant interaction between any covariate and month on the species assemblage structure was detected via the MANCOVA procedure (Table 7). Fish assemblage structure did not differ among monthly samples. Fish assemblage structure differed significantly along a longitudinal gradient of pool size (PC1) but was not affected by the environmental covariates of current velocity and temperature (PC2), depth and conductivity (PC3) or dissolved oxygen (PC4). The detection of a spatial effect of pool size on the species assemblages in the absence of an effect due to month or an interaction between month and any covariate indicates that the spatial differences in the assemblage structure were temporally constant.

Species Correlations with Environmental Variables

Because PCA determined large woody material and canopy coverage were not important in structuring deep pool habitats, I removed these two variables from the environmental matrix for CCA analysis. Inclusion of these variables had no effect on the

outcome of the CCA. In addition, due to the multicollinearity problems associated with depth, area, and volume, I removed volume from the analysis. Choosing to remove volume allowed the ordination to still contain depth, area, and width that combined represent volume without problems with multicollinearity.

The eigenvalues for the three canonical axes calculated by CCA were 0.209, 0.146, and 0.102 resulting in 5.9%, 4.1%, and 2.9%, respectively, of total variance in the assemblage data explained by the linear combinations of the measured environmental variables along each respective axis (Table 8). The eigenvalue for axis 1 was significant ($P = 0.002$) based on the Monte Carlo randomization procedure indicating that this eigenvalue was greater than expected by chance. Conductivity, temperature, width, area, elevation, and dissolved oxygen were correlated with axis 1. Axis 2 contributed to a similar amount of variation explained in the species data (4.1%) as axis 1. Current velocity descriptors were correlated with axis 2. Though mean current velocity had a correlation with axis 1 greater than 0.32, it had a higher correlation with axis 2 and thus is considered to be correlated with axis 2. This was also the case for dissolved oxygen but with a higher correlation with axis 1 than axis 2. Axis 3 had no interpretable correlations with any of the environmental variables and explained little variation in the species data.

Only the first two axes produced interpretable results, therefore only these axes were plotted in the biplot (Figure 5). The vectors for dissolved oxygen and elevation display the positive correlations between these variables and the first canonical axis. Area, conductivity, temperature, and width vectors represent the strength and direction of the correlations between these variables and axis 1. Axis 2 had a positive correlation

with mean current velocity and a negative correlation with variation in current velocity represented by their environmental vectors.

Species abundances within sample units appear to be correlated with a longitudinal gradient in pool size (Figure 7). Species plotted to the far right along axis 1, indicating their increasing association with smaller, higher elevation pools, were highfin carpsucker *Carpiodes velifer*, freshwater drum, spotted bass *Micropterus punctulatus*, common carp *Cyprinus carpio*, blacktail redhorse *Moxostoma poecilurum*, and channel catfish *Ictalurus punctatus*. Smallmouth buffalo and minnows were just to the right along axis one and quillback carpsuckers *Carpiodes cyprinus* and spotted gar *Lepisosteus oculatus* were just to the left of this axes representing their greater abundances in middle elevation pools of moderate size. Longnose gar, river carpsucker, flathead catfish, and gizzard shad *Dorosoma cepedianum* were associated with larger, downstream pools. In addition to associations with pool size and location, species displayed associations with current velocity descriptors and other environmental variables. Smallmouth buffalo appeared to be associated with moderate to fast current velocities, whereas minnows appeared to be associated with more variable current velocities. Spotted bass appeared to be associated with elevated dissolved oxygen concentrations and faster current velocities, whereas longnose gar, river carpsucker, and flathead catfish were associated with slower current velocities and warmer temperatures.

CHAPTER IV

DISCUSSION

Pioneers in river morphology (e.g., Leopold et al. 1964) noted that as a river follows its downstream path it increases in size (e.g., width) to compensate for the increase in amount of water from increases in drainage area and tributary inputs. Principal component analysis of the measured environmental variables detected this trend and identified the increase in pool width, area, and volume with a decrease in elevation as the source of the greatest amount of variation in habitat conditions of deep pool habitats of the UTR. Though the change in elevation along the 100-km UTR was only 30 m, this change coupled with the increase in the size of the pools was so great that these variables together explained more than 40% of the variation in habitat conditions of deep pools.

Variations in current velocity and temperature are a function of seasonal changes in weather patterns. Although I attempted to sample at relatively similar river stages, variations in current velocities were measurable and were probably due to seasonal differences in precipitation. In the warmer, drier summer months typical of northern Mississippi, discharge is reduced, whereas in cooler late winter and early spring, precipitation events increase discharge throughout the watershed. Mean annual

precipitation in Mississippi is 142 cm and in 2004, Mississippi received a total rainfall amount of about 157 cm (http://www.ncdc.noaa.gov). Therefore during this study, Mississippi experienced a somewhat wet year and generalizations made from this study may not be applicable during extreme drought years when low water conditions inhibit fish movement among habitats.

Expected variations in temperature also occurred. There was a high amount of variation in current velocity and temperature, but these variables varied about the same in each pool; the ranges of mean current velocity (0.03 and 0.72 m/sec) and mean temperature (8.8 and 31.0 C) though large, explained half of the variation in habitat conditions among sample units relative to that explained by longitudinal position and size of pool. Although conductivity, depth, and dissolved oxygen varied across sample units, these variables together accounted for only 18% of additional variation in habitat conditions of deep pools. Canopy coverage and large woody materials, although variable across pools, provided no explanation of the variation of habitat conditions. Synthesizing these results, it is concluded that the spatial variation in pool size along an elevation gradient superseded other measured physicochemical variables as the dominant factor defining deep pool habitat.

In warmwater streams the fish assemblages, although rich in species, often are numerically dominated by a few species (Evans and Noble 1979; Schlosser 1987; Meffe and Sheldon 1988). This was the case in this study as well. As identified by NMS, the fish assemblage structure of the pools was influenced strongly by the abundances of smallmouth buffalo, flathead catfish, longnose gar, freshwater drum and minnow species.

Schlosser (1987) suggested a theoretical framework from which stream ecologists can develop hypotheses regarding species distributions along different levels of habitat complexity. Systems with little anthropogenic impact displayed large variability in available habitat types and longitudinal differences in the structure of fish assemblages. The patterns in assemblage structure were thought to be temporally constant regardless of complex environmental conditions. In contrast, Schlosser (1987) suggested that assemblages exposed to extreme environmental variability (e.g., altered hydrographs, Oberdoff et al. 2001; Pegg and Pierce 2002; Adams et al. 2004) often display temporal variation in structure. Although the watershed in this study has been modified by the creation of the TTW, the temporally stable fish assemblage structure of deep pools in the UTR suggests that the little instream alteration that has occurred within the UTR is not extreme enough to elicit temporal changes in the structure of the assemblages that occupy deep pools.

The fish assemblage structure in deep pools of the UTR was related significantly to pool size and location and little related to the other covariates that were indicative of seasonal changes in variables such as temperature, dissolved oxygen, and current velocity. In streams similar to the UTR with little or no human alteration, the structure of the assemblages depends on stream size while independent of seasonal variation in temperature and flow regimes (Matthews 1986; Matthews et al. 1988; Meador and Matthews 1992). The results of the present study also corroborate findings of Taylor (2000) that pool assemblage structure is more predictable along elevation gradients than

along temporally changing environmental gradients and the conclusions of Gelwick (1990) and Matthews et al. (1994b) that the spatial arrangement of the fish assemblages of pools is relatively stable over time.

The CCA biplot revealed the directional relationship between pool size and location with the fish assemblage structure of deep pools that could not be deduced from the MANCOVA results. A shift in assemblages characterized by the abundances of species such as longnose gar and flathead catfish to assemblages characterized by species such as smallmouth buffalo, minnows, and freshwater drum occurred from low elevation pools to higher elevation pools. Flathead catfish and longnose gar were typically the larger-bodied fish sampled in this study, and these species not only increased in abundance but increased in their frequency of occurrence in the larger, downstream pools (Table 3). A shift to assemblages characterized by species such as smallmouth buffalo and minnows occurred along an increase in elevation that matched their greater abundance and frequency of occurrence in the upstream pools. All but three freshwater drum were captured in pools 1-9 (Table 3) and this species association with higher elevation pools was evident in the CCA biplot

Though the measured environmental variables may have provided a statistically significant contribution to the explanation of the variation in the structure of the fish assemblages in deep pools as indicated in the MANCOVA results, the contribution of these variables in explaining variation in the assemblage structure was relatively small in relation to the total variation that could potentially have been explained as indicated in the CCA results. All measured variables combined (excluding canopy coverage and

large woody materials) explained only a portion (10% along the first two canonical axes) of the total variation in the assemblages. Although the measured environmental variables such as pool size, location, temperature, and current velocity displayed a high degree of spatial and temporal variation as indicated by their explanation of the habitat conditions of deep pools, they may not have been the most important factors causing changes in fish assemblage structure across sample units. This suggests that either the physicochemical variables measured were not of strong importance to the distribution of fishes or that other factors such as biotic interactions were occurring that elicited the observed patterns in assemblage structure. Therefore a substantial and possibly ecologically significant amount of variation in the assemblages of deep pools was not accounted for in this study.

A relevant objective to the investigation of deep pool habitats and their relationships to the species occupying them is to determine if these habitats serve some important function to the existence of particular species. Pools of the UTR were thought to provide critical habitat for Gulf Coast walleye. Schultz (1971) described habitat used by walleye in the UTR as deep areas that provided a diverse range of velocity regimes and low light penetration. Extensive sampling for this study and for collection of broodstock collected walleye only in upstream portions of the UTR (personal observation). Unfortunately, only one individual was caught during this study. This individual was captured in the October sample at pool 4 approximately 1 km downstream of the Walker's Bridge boat ramp. The habitat conditions of this pool (see Table 1) and other pools in the upper portion of the UTR where walleye were captured during broodstock collection efforts were similar to those described by Schultz (1971) as

preferred walleye habitat in the Tombigbee River drainage. Nevertheless, the limited captures preclude any conclusions about the value of deep pools to this apparently rare fish.

In conclusion, it appears that the structure of the fish assemblages occupying deep pools in the UTR changes along an elevation gradient of pool size and this relationship is temporally stable. The River Continuum Concept (Vannote et al. 1980) states that the structure of fish assemblages changes along the downstream gradient of a river. Schlosser (1982) validated this concept by showing that the assemblage structure of more environmentally stable pools downstream in a small warmwater stream was different from those in the more hydrologically variable habitats upstream owing to different functional groups of species. Differences among assemblages along some spatial gradient independent of habitat conditions have been postulated to be the product of biotic factors such as predation (Angermeier and Karr 1983) and competition (Matthews et al. 1994b). The relatively small amount of variation in the occurrences and abundances of species in deep pools that was explained by the environmental variables suggests other processes may also be important in producing the observed change in the assemblage structure along an elevation gradient. From an ecological and management perspective, it may be of interest to determine what the relative contribution of biological interactions is over abiotic habitat conditions to the development of the structure of fish assemblages in warmwater streams. Ecologists may then have a better understanding of not just the structure of the assemblages, but the functional role of fishes play in the

assemblages in deep pools. Although the goal of this research was to identify the structure, not the functional organization, of the fish assemblages of deep pools, this study produces new hypotheses concerning the ecology of fish occupying deep pools of warmwater rivers and streams.

LITERATURE CITED

Aadland, L.P. 1993. Stream habitat types: their fish assemblages and relationship to flow. North American Journal of Fisheries Management 13: 790-806.

Adams, S.B., M.L. Warren Jr., and W.R. Haag. 2004. Spatial and temporal patterns in fish assemblages of upper coastal plain streams, Mississippi, USA. Hydrobiologia 528: 45-61.

Angermeier, P.L. 1987. Spatiotemporal variation in habitat selection by fishes in small Illinois streams. Pages 52-60 *in* W.J. Matthews and D.C. Heins, editors. Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press, Norman, Oklahoma, USA.

Angermeier, P.L. and J.R. Karr. 1983. Fish communities along environmental gradients in a system of tropical streams. Environmental Biology of Fishes 9(2): 117-135.

Barbour, M.T., J. Gerritsen, B.D. Snyder, and J.B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: Periphyton, benthic macroinvertebrates and fish, second edition. EPA 841-B-99-002. U.S. Environmental Protection Agency; Office of Water; Washington, D.C., USA.

Boschung, H. 1987. Physical factors and the distribution and abundances of fishes in the Upper Tombigbee River system of Alabama and Mississippi, with emphasis on the Tennesee-Tombigbee Waterway. Pages 184-192 *in* W.J. Matthews and D.C. Heins, editors Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press, Norman, Oklahoma, USA.

Burkhardt, R.W., and S. Gutreuter. 1995. Improving electrofishing catch consistency by standardizing power. North American Journal of Fisheries Management 15: 375-381.

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

Ebersole, J.L., W.J. Liss, and C.A. Frissell. 2003. Cold water patches in warm streams: physicochemical characteristics and the influence of shading. Journal of the American Water Resources Association 39(2):355-368.

ESRI. 2002. Getting to know ArcGIS desktop. Environmental Systems Research Institute, Inc. Redlands, California, USA.

Evans, J.W., and R.L. Noble. 1979. The longitudinal distribution of fishes in an east Texas stream. American Midland Naturalist 101(2): 333-343.

Fraser, D.F., D.A. DiMattia, and J.D. Duncan. 1987. Living among predators: the response of a stream minnow to the hazard of predation. Pages 121-127 *in* W.J. Matthews and D.C. Heins, editors Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press, Norman, Oklahoma, USA.

Gelwick, F.P. 1990. Longitudinal and temporal comparisons of riffle and pool fish communities in a northeastern Oklahoma Ozark stream. Copeia 1990(4):1072-1082.

Gelwick, F.P., S. Akin, D.A. Arrington, and K.O. Winemiller. 2001. Fish assemblage structure in relation to environmental variation in a Texas Gulf Coastal wetland. Estuaries 24(2): 285-296.

Gorman, O.T., and J.R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59:507-515.

Hair, J.F., Jr., R.E. Anderson, and R.L. Tatham. 1987. Mulitvariate Data Analysis, second edition. Macmillian, New York, New York, USA.

Horwitz, R.J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecological Monographs 48: 307-321.

Jackson, D.A., P.R. Peres-Neto, J.D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquaculture Sciences 58: 157:170.

Kingery, R.W., and R.J. Muncy. 1990. Walleye spawning, movements and habitat usage in Tombigbee River drainages. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 42:249-257.

Kruskal, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29: 115-129.

Kwak, T.J. 1991. Ecological characteristics of a northern population of the pallid shiner. Transactions of the American Fisheries Society 120: 106-115.

Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. Fluvial Processes in Geomorphology. W.H. Freeman and Company. San Francisco, California, USA.

Lewis, W.M. 1978. Comparison of temporal and spatial variation in the zooplankton of a lake by means of variance components. Ecology 59: 666-671.

Lobb, M.D., and D.J. Orth. 1991. Habitat use by an assemblage of fish in a large warmwater stream. Transactions of the American Fisheries Society 120: 65-78.

Marsh-Matthews, E., and W.J. Matthews. 2000. Geographic, terrestrial and aquatic factors: which most influence the structure of stream fish assemblages in the midwestern United States? Ecology of Freshwater Fish. 9: 9-21.

Matthews, K.R., N.H. Berg, D.L. Azuma, and T.R. Lambert. 1994a. Cool water formation and trout habitat use in deep pools in the Sierra Nevada, California. Transactions of the American Fisheries Society 123:549-564.

Matthews, W.J. 1986. Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood. Copeia 1986(2):388-397.

Matthews, W.J. 1990. Spatial and temporal variation in fishes of riffle habitats: a comparison of analytical approaches for the Roanoke River. American Midland Naturalist 124: 31-45.

Matthews, W.J., R.C. Cashner, and F.P. Gelwick. 1988. Stability and persistence of fish faunas and assemblages in three midwestern streams. Copeia 1988(4):945-955.

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

Matthews, W.J., A.J. Stewart, and M.E. Power. 1987. Grazing fishes as components of North American stream ecosystems: effect of *Campostoma anomalum*. Pages 128-143 *in* W.J. Matthews and D.C. Heins, editors Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press, Norman, Oklahoma, USA.

McCune, B., and J.B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Glenden Beach, Oregon, USA.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data. Version 4.38. MjM Software, Glenden Beach, Oregon, U.S.A.

McGarigal, K., S. Cushman, and S. Stafford. 2000. Ordination: Principal Components Analysis pp. 19-78 *in* Multivariate Statistics for Wildlife and Ecology Research. Springer Science+Buisness Media, New York, NY, USA.

McMahon, T.E., A.V. Zale, and D.J. Orth. 1996. Aquatic habitat measurements. Pages 83-120 *in* B.R. Murphy and D.W. Willis, editors Fisheries Techniques second edition. American Fisheries Society, Bethesda, MD.

Meador, M.R., and W.J. Matthews. 1992. Spatial and temporal patterns in fish assemblage structure of an intermittent Texas stream. American Midland Naturalist 127: 106-114.

Meffe, G.K, and A.L. Sheldon. 1988. The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. The American Midland Naturalist 120:225-240.

Nielsen, J.L., T.E. Lisle, and V. Ozaki. 1994. Thermally stratified pools and their use by steelhead in northern California streams. Transactions of the American Fisheries Society 123:613-626.

Oberdorff, T., B. Hugueny, and T.Vigneron. 2001. Is assemblage variability related to environmental variability? An answer for riverine fish. Oikos. 93:419-428.

Pegg, M.A., and C.L. Pierce. 2002. Fish community structure in the Missouri and lower Yellowstone rivers in relation to flow characteristics. Hydrobiologia 479:155-167.

Pugh, L.L., and H.L. Schramm, Jr. 1998. Comparison of electrofishing and hoopnetting in lotic habitats of the lower Mississippi River. North American Journal of Fisheries Management 18: 649-656.

Peterson, J.T., and C.F. Rabeni 1995. Optimizing sampling effort for sample warmwater stream fish communities. North American Journal of Fisheries Management 15: 528-541.

Peterson, J.T., and C.F. Rabeni. 2001. The relation of fish assemblages to channel units in an Ozark stream. Transactions of the American Fisheries Society 130:911-926.

Quist, M.C., J.S. Tillma, M.N. Burlingame, and C.S. Guy. 1999. Overwinter habitat use of shovelnose sturgeon in the Kansas River. Transactions of the American Fisheries Society 128:522-527.

Rabeni, C.F., and R.B. Jacobson. 1999. Warmwater Streams. Pages 505-528. *in* C.C. Kohler and W.A. Hubert, editors. Inland Fisheries Management in North America, second edition. American Fisheries Society, Bethesda, Maryland.

Reynolds, J.B. 1996. Electrofishing. Pages 221-254. *in* B.R. Murphy and D.W. Willis, editors. Fisheries Techniques, second edition. American Fisheries Society, Bethesda, Maryland.

Robertson, M.S., and K.O. Winemiller. 2003. Habitat associations of fishes in the Devil's River, Texas. Journal of Freshwater Ecology 18:115-127.

Ross, S.T. 2001. The inland fishes of Mississippi. Mississippi Department of Wildlife, Fisheries and Parks, Jackson.

SAS Institute. 1985. SAS user's guide: statistics. SAS Institute, Cary, North Carolina.

Schaefer, J. 2001. Riffles as barriers to interpool movement by three cyprinids (*Notropis boops, Campostoma anomalum* and *Cyprinella venusta*). Freshwater Biology 46: 379-388.

Schlosser, I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs 52: 395-414.

Schlosser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17-24 *in* W.J. Matthews and D.C. Heins, editors Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press, Norman, Oklahoma, USA.

Schofield, P.J., and S.T. Ross. 2003. Habitat selection of the channel darter *Percina* (Cottogaster) *copelandi*; a surrogate for the imperiled pearl darter *Percina aurora*. Journal of Freshwater Ecology 18(2): 249-258.

Schramm, H.L., Jr., and L.E. Miranda. 2001. A conservation and management plan for the Gulf Coast strain walleye. Mississippi Department of Wildlife, Fisheries, and Parks, Jackson.

Schultz, C.A. 1971. Survey of walleye population and related parameters in the Tombigbee River system in Mississippi. Mississippi Fish and Game Commission. Final Report, Project F-23, Jackson.

SPSS for Windows. Release 10.0.5 1999. SPSS Inc., Chicago, Illinois, USA.

Taylor, C.M. 2000. A large-scale comparative analysis of riffle and pool fish communities in an upland stream system. Environmental Biology of Fishes 58:89-95.

Thompson, A.R., J.T. Petty, and G.D. Grossman. 2001. Multi-scale effects of resource patchiness on foraging behaviour and habitat use by longnose dace, *Rhinichthys cataractae*. Freshwater Biology 46: 145-160.

Vannote, R.L., G.W. Minshall, K.W. Cummings, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences. 37:130-137.

Table 1. Environmental conditions for 14 sampled pools on the Upper Tombigbee River averaged across all sampling occasions from March 2004 to March 2005. See text for pool locations.

	Pool							
Variable	1	2	3	4	5	7	8	9
River mile (km)	99.7	98.8	98.5	98.1	97.9	39.2	38.9	38.6
Elevation (m)	88	87	87	87	87	72	72	72
Area (m2)	568.6	1612.7	693.4	1212.9	881.2	2378.8	2632.1	3812.5
Width (m)	10.2	22.3	11.3	12.7	14.5	27.3	23.0	20.7
Mean volume (m3)	1303.6	3391	1715.6	3033.6	1464.9	5374.2	6323.8	10818.2
Range of mean depth (m)	1.34-3.25	1.80-2.45	2.03-2.93	2.10-3.03	1.28-2.12	1.56-2.73	1.45-2.86	2.18-3.55
Mean LWM (%)	28.6	6.7	26.7	25.0	33.3	5.0	15.0	25.0
Mean canopy coverage (%)	33.1	1.0	59.4	46.3	48.3	30.0	44.3	63.3
Range of conductivity (µS/cm)	39.0-85.4	39.1-86.6	39.6-86.2	39.5-86.3	39.7-85.6	74.3-94.9	74.2-111.9	74.2-117.0
Range of mean current velocity (m/sec)	0.10-0.26	0.06-0.34	0.12-0.23	0.13-0.20	0.10-0.34	0.13-0.27	0.17-0.36	0.14-0.36
Range of mean temperature (C)	8.8-27.8	9.0-26.5	9.2-26.3	9.4-26.8	9.6-27.3	12.8-25.4	12.8-25.7	12.9-26.1
Range of mean dissolved oxygen (mg/L)	5.5-9.5	5.5-9.3	5.1-8.0	5.5-9.5	5.4-9.5	6.6-8.6	6.5-9.3	6.2-9.3

Table 1 con't. Environmental conditions for 14 sampled pools on the Upper Tombigbee River averaged across all sampling occasions from March 2004 to March 2005. See text for pool locations.

	Pool					
Variable	10	11	12	13	14	15
River mile (km)	9.3	8.6	8.2	7.6	7.1	6.6
Elevation (m)	60	59	58	58	58	58
Area (m2)	1992.5	2123.2	3109.8	9816.5	7177.5	12695.0
Width (m)	24.7	35.7	38.4	68.6	62.1	67.6
Mean volume (m3)	5127.7	5925.7	12478.3	28346.3	21354.9	43465.3
Range of mean depth (m)	2.16-3.24	2.19-3.40	3.44-4.50	2.10-3.26	2.36-3.20	2.72-4.22
Mean LWM (%)	14.2	10.8	9.2	10.8	25.0	24.0
Mean canopy coverage (%)	9.9	11.9	10.1	0.8	1.1	1.7
Range of conductivity (µS/cm)	62.8-95.8	63.3-95.6	63.6-93.9	85.0-222.1	76.8-158.7	102.1-144.4
Range of mean current velocity (m/sec)	0.20-0.72	0.08-0.32	0.07-0.31	0.03-0.32	0.06-0.30	0.09-0.33
Range of mean temperature (C)	10.4-30.8	10.6-31.0	10.7-30.1	10.7-30.1	11.1-30.0	11.1-30.0
Range of mean dissolved oxygen (mg/L)	3.6-9.3	3.6-9.0	4.1-8.9	4.3-9.7	4.3-9.6	3.9-9.2

Table 2. Species occurrences (N) and relative abundances in 14 deep pools of the Upper Tombigbee River sampled from March 2004 to March 2005 (percentage of total catch, %). (n = 84).

Scientific Name	Common Name	N	%
Ichthyomyzon cataneus [a]	Chestnut lamprey	1	0.26
Lepisosteus oculatus	Spotted gar	6	1.12
Lepisosteus osseus	Longnose gar	47	10.06
Lepisosteus platostomus	Shortnose gar	4	0.77
Dorosoma cepedianum	Gizzard shad	22	3.14
Dorosoma petenense	Threadfin shad	3	0.46
Cyprinidae [b]	Minnow	55	13.15
Cyprinus carpio	Common carp	11	2.59
Carpiodes carpio	River carpsucker	53	8.18
Carpiodes cyprinus	Quillback carpsucker	20	5.42
Carpiodes velifer	Highfin carpsucker	10	1.29
Ictiobus bubalus	Smallmouth buffalo	123	26.94
Moxostoma poecilurum	Blacktail redhorse	5	0.98
Ictalurus furcatus	Blue catfish	3	0.58
Ictalurus punctatus	Channel catfish	14	3.38
Pylodictis olivaris	Flathead catfish	51	12.06
Morone chrysops	White bass	2	0.55
Lepomis macrochirus	Bluegill	4	0.96
Lepomis megalotis	Longear sunfish	1	0.11
Micropterus punctulatus	Spotted bass	8	2.19
Micropterus salmoides	Largemouth bass	1	0.20
Pomoxis annularis	White crappie	1	0.60
Pomoxis nigromaculatus	Black crappie	2	0.32
Sanders vitreous [a]	Walleye	1	0.36
Aplodinotus grunniens	Freshwater drum	20	4.29
Total		468	

[a] Species of special concern

[b] Members of the Minnow group were: blacktail shiner, Silvery shiner, Unknown shiner and pretty shiner.

Table 3. Distribution of the 14 common species sampled in deep pools of the Upper Tombigbee River from March 2004 to March 2005. Values outside parentheses represent total number of that species caught for a particular pool. Number inside parentheses represents number of dates when the species was caught and n is number of times (sampling dates) pool was sampled.

	Pool													
	1	2	3	4	5	7	8	9	10	11	12	13	14	15
Species	n = 7	n = 6	n = 6	n = 6	n = 6	n = 4	n = 7	n = 7	n = 6	n = 6	n = 6	n = 6	n = 6	n = 5
Spotted gar							3(3)	2(2)	1(1)					
Longnose gar	1(1)	3(2)			2(1)		19(4)	6(3)	1(1)	3(1)	2(2)	6(3)	1(1)	3(2)
Gizzard shad		2(1)				1(1)						2(1)	16(2)	1(1)
Minnow	4(2)	10(5)	9(4)	8(3)			1(1)	4(3)		8(4)	3(2)	2(2)	5(1)	1(1)
Common carp		1(1)	4(2)	2(1)	1(1)			1(1)		1(1)				1(1)
River carpsucker	1(1)		2(2)		1(1)	4(1)	5(2)	13(3)	1(1)	1(1)	3(2)	2(2)		20(4)
Quillback carpsucker	2(1)	2(2)	1(1)	2(2)	1(1)		6(3)	4(2)				1(1)		1(1)
Highfin carpsucker		1(1)	1(1)					7(3)						1(1)
Smallmouth buffalo	10(5)	9(4)	2(2)	11(4)	10(4)	5(3)	20(5)	17(6)	7(5)	6(4)	6(4)	7(2)	5(2)	8(3)
Blacktail redhorse		1(1)		1(1)		1(1)		2(1)						
Channel catfish	2(2)	3(1)	1(1)	5(3)					1(1)	1(1)		1(1)		
Flathead catfish	1(1)			1(1)	4(3)		1(1)	4(3)	6(4)	5(3)	11(3)	7(3)	4(2)	7(4)
Spotted bass	1(1)		1(1)		1(1)	1(1)	1(1)		2(1)	1(1)				
Freshwater drum	4(2)	3(3)		4(2)	1(1)	1(1)	1(1)	2(2)		2(1)				2(2)

Table 4. Environmental variable loadings on the first four axes calculated by principal components analysis of 13 environmental variables measured in 14 deep pools of the Upper Tombigbee River from March 2004 to March 2005.

	Axis			
Variable	1	2	3	4
Large woody materials	0.14	-0.22	0.23	-0.05
Canopy	0.25	0.10	0.12	-0.19
Conductivity	-0.27	0.24	0.41	0.08
Mean depth	-0.29	-0.22	-0.44	-0.23
Maximum depth	-0.30	-0.14	-0.47	-0.28
Current velocity	0.15	-0.44	0.26	-0.36
CV current velocity	-0.08	0.48	-0.33	0.26
Temperature	-0.12	0.51	0.18	-0.30
Dissolved oxygen	0.09	-0.29	-0.07	0.71
Width	-0.40	-0.07	0.17	0.15
Area	-0.39	-0.10	0.27	0.09
Volume	-0.40	-0.15	0.11	0.01
Elevation	0.38	0.09	-0.10	0.00

Table 5. Results of non-metric multidimensional scaling procedure used to find a suitable final solution of an ordination of the abundances of the 14 most abundant species sampled from 14 deep pools of the Upper Tombigbee River from March 2004 to March 2005.

Axes in solution	Stress in real data			Stress in randomized data			
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
1	42.45	52.14	56.60	44.96	51.92	56.60	0.0196
2	24.89	25.67	29.38	25.52	28.16	40.95	0.0196
3	17.55	17.84	18.56	17.26	19.04	20.69	0.0392
4	12.82	13.59	26.25	12.85	14.63	28.84	0.0196
5	9.83	9.95	10.82	9.74	10.83	13.10	0.0588
6	7.80	7.89	8.10	7.64	8.48	9.25	0.0784

Table 6. Species correlations with significant axes and percent of variation in species data explained by each axis calculated by non-metric multidimensional scaling of the 14 most abundant species sampled in 14 deep pools of the Upper Tombigbee River from March 2004 to March 2005.

	Axis		
Species	1	2	3
Spotted gar	-0.03	-0.11	-0.10
Longnose gar	-0.60	-0.28	0.12
Gizzard shad	-0.05	-0.35	-0.05
Minnow	0.34	0.37	0.57
Common carp	0.27	0.13	0.16
River carpsucker	-0.33	0.06	0.31
Quillback carpsucker	0.07	-0.31	-0.01
Highfin carpsucker	0.02	0.11	0.15
Smallmouth buffalo	0.36	-0.07	-0.70
Blacktail redhorse	0.21	-0.10	0.03
Channel catfish	0.29	0.19	0.13
Flathead catfish	-0.69	0.38	0.21
Spotted bass	0.13	0.37	-0.14
Freshwater drum	0.34	-0.44	0.33
% Of species data explained	23.3	19.1	33.8

Table 7. Results of the MANCOVA test for temporal differences in fish assemblage structure in response to environmental covariates in 14 sampled deep pools of the Upper Tombigbee River from March 2004 to March 2005. See text for description of covariates.

Effect	F	df	p
PC1*month	0.91	18, 119.28	0.5714
PC2*month	0.72	18, 119.28	0.7798
PC3*month	1.47	18, 119.28	0.1127
PC4*month	0.92	18, 119.28	0.5531
month	1.50	18, 187.16	0.0920
PC1	7.38	3, 66	0.0002
PC2	1.54	3, 66	0.2172
PC3	2.62	3, 66	0.0578
PC4	1.46	3, 66	0.2331

Table 8. Intraset environmental correlations calculated for 14 sampled deep pools of the Upper Tombigbee River from March 2004 to March 2005 using canonical correspondence analysis. Percent of variation explained describes the amount of variation in species data explained by the measured environmental variables.

	Axis		
Environmental variable	1	2	3
Area	-0.66	0.02	-0.07
Width	-0.66	-0.09	-0.21
Elevation	0.64	0.10	-0.10
Mean depth	-0.17	-0.16	-0.12
Maximum depth	-0.20	-0.28	0.01
Mean current velocity	0.34	0.57	0.04
C.V. current velocity	-0.18	-0.59	-0.21
Conductivity	-0.90	0.24	0.12
Temperature	-0.76	-0.21	0.20
Dissolved oxygen	0.59	0.42	0.15
Eigenvalue	0.209	0.146	0.102
% Variation explained	5.9	4.1	2.9

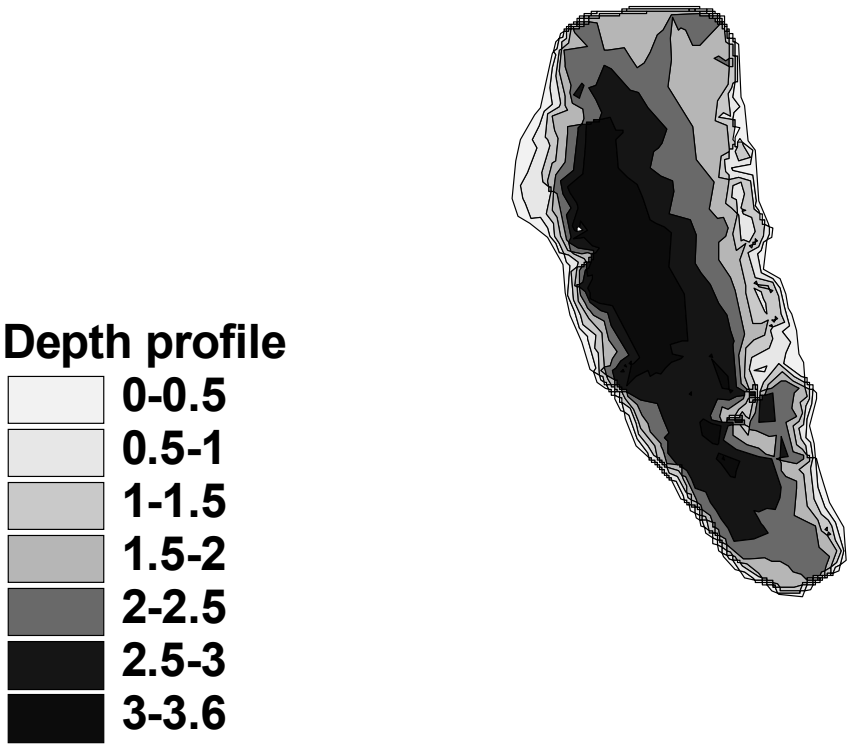

Figure 1. Example of a bathymetric map created from sonar data collected in a deep pool of the Upper Tombigbee River used to calculate pool area, volume and mean and maximum depth. Depths are in meters.

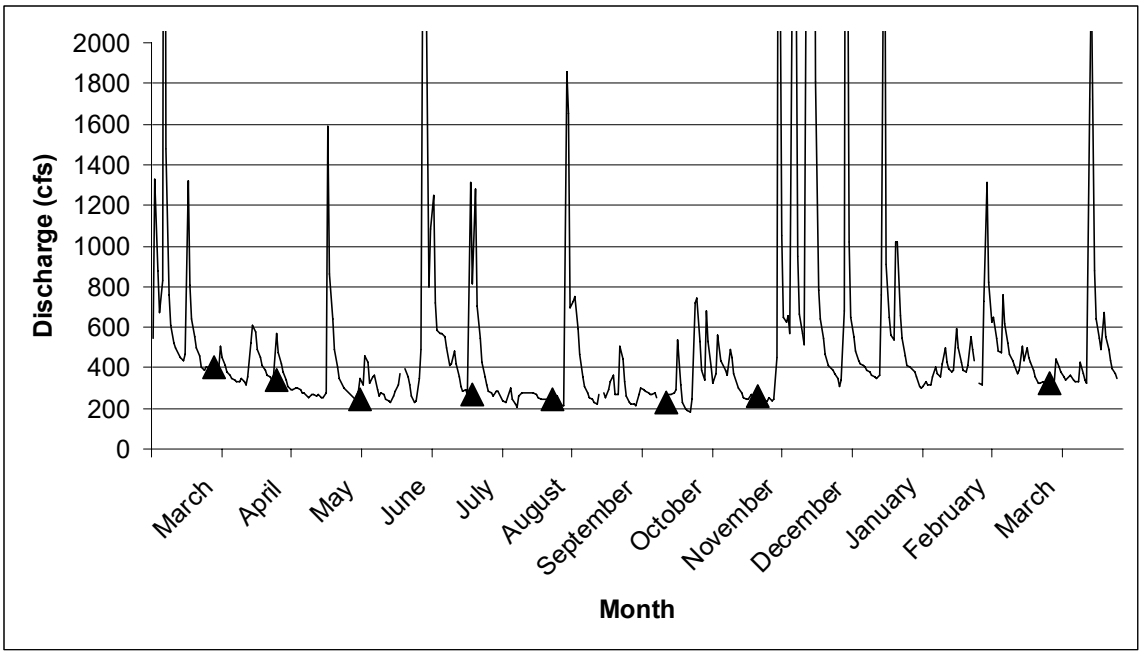

Figure 2. Discharge data from the USGS gaging station on the Upper Tombigbee River at Marietta, Mississippi (02430500) recorded from March 2004 to April 2005. Triangles (▲) indicate sampling dates.

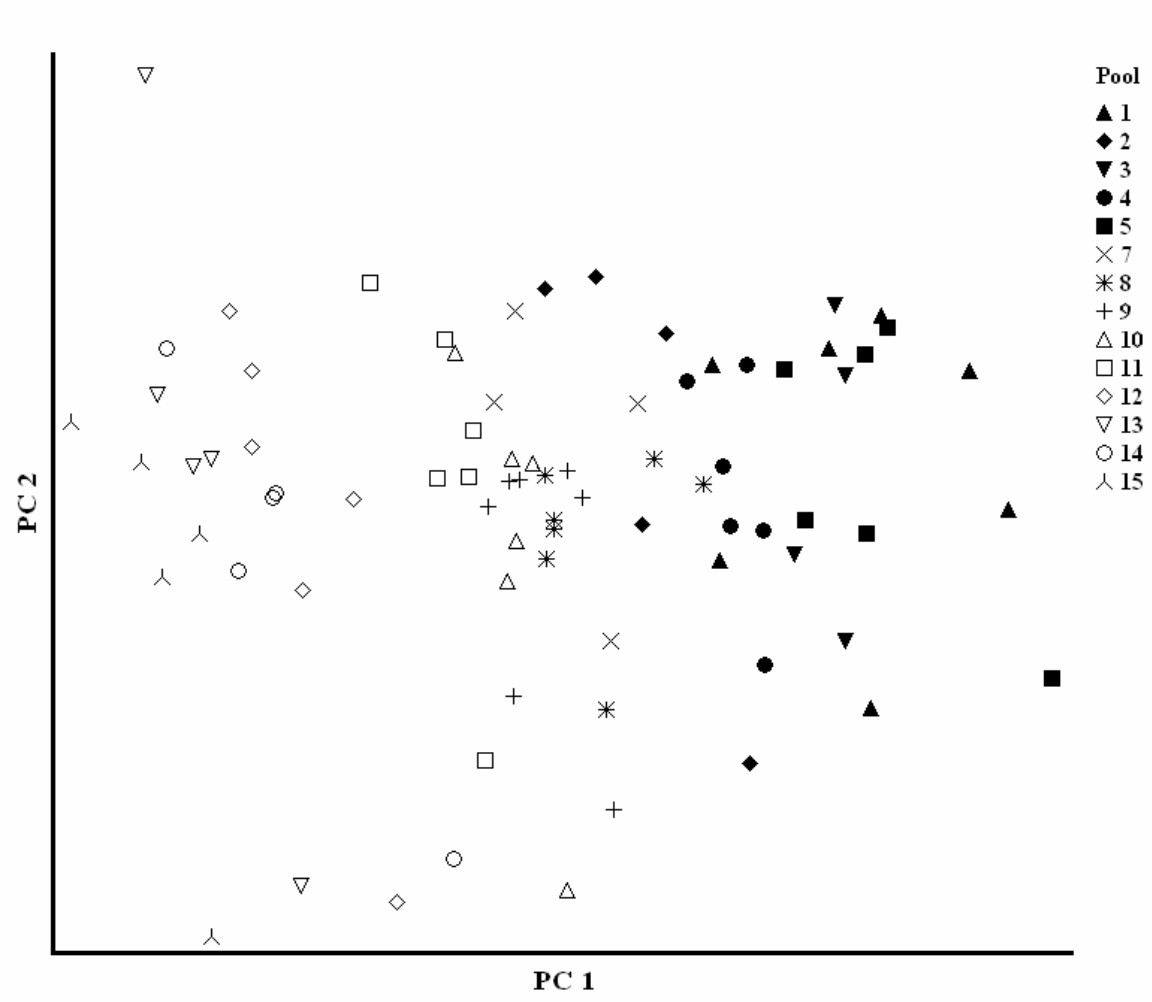

Figure 3. Plot of samples along the first two axes produced by principal components analysis of environmental conditions of deep pools (n = 79) in the Upper Tombigee River from March 2004 to March 2005. Axis one (principal component 1, horizontal axis) represents an increase in pool size as elevation decreases. Axis two (principal component 2, vertical axis) represents an increase in current velocity as temperature decreases.

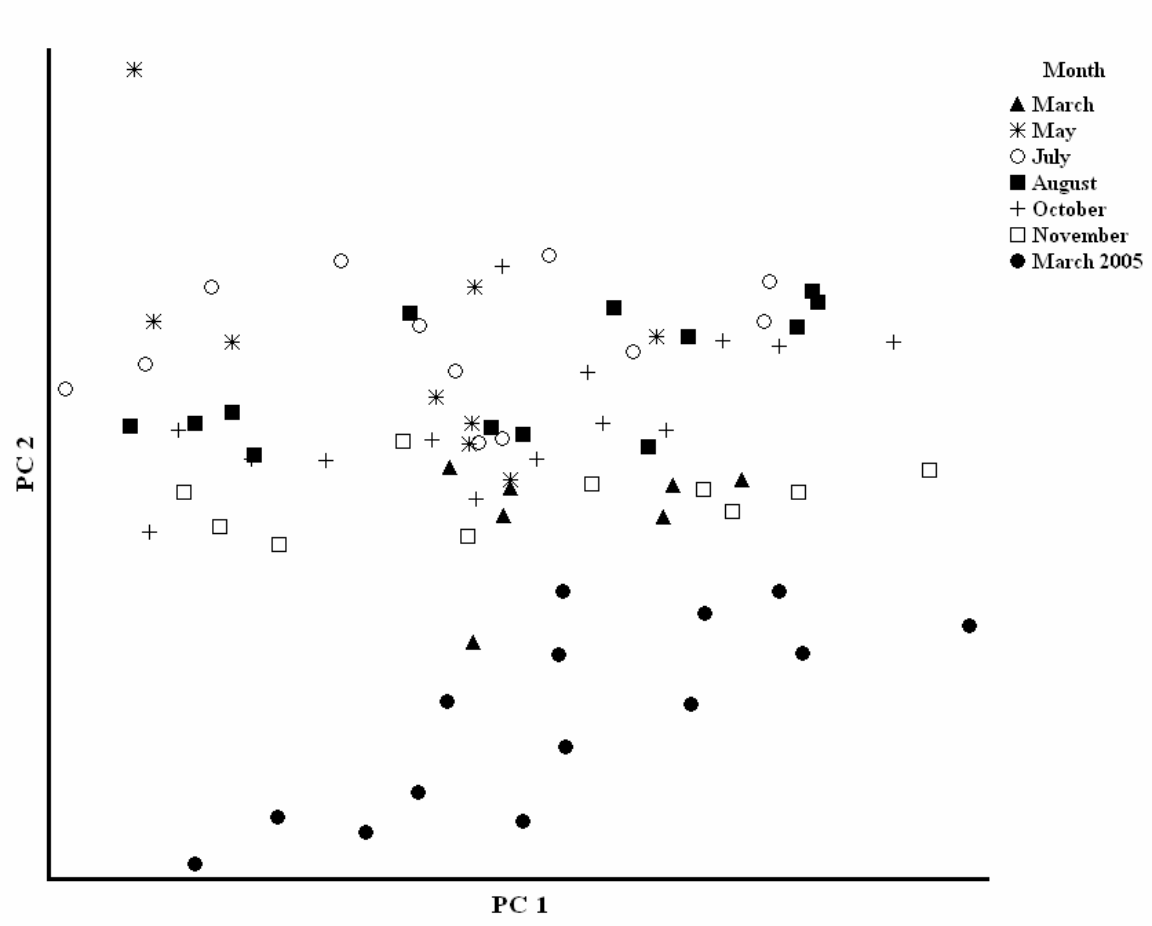

Figure 4. Plot of samples along the first two axes produced by principal components analysis of environmental conditions of deep pools (n = 79) in the Upper Tombigbee River from March 2004 to March 2005. Axes are those as described in figure 3.

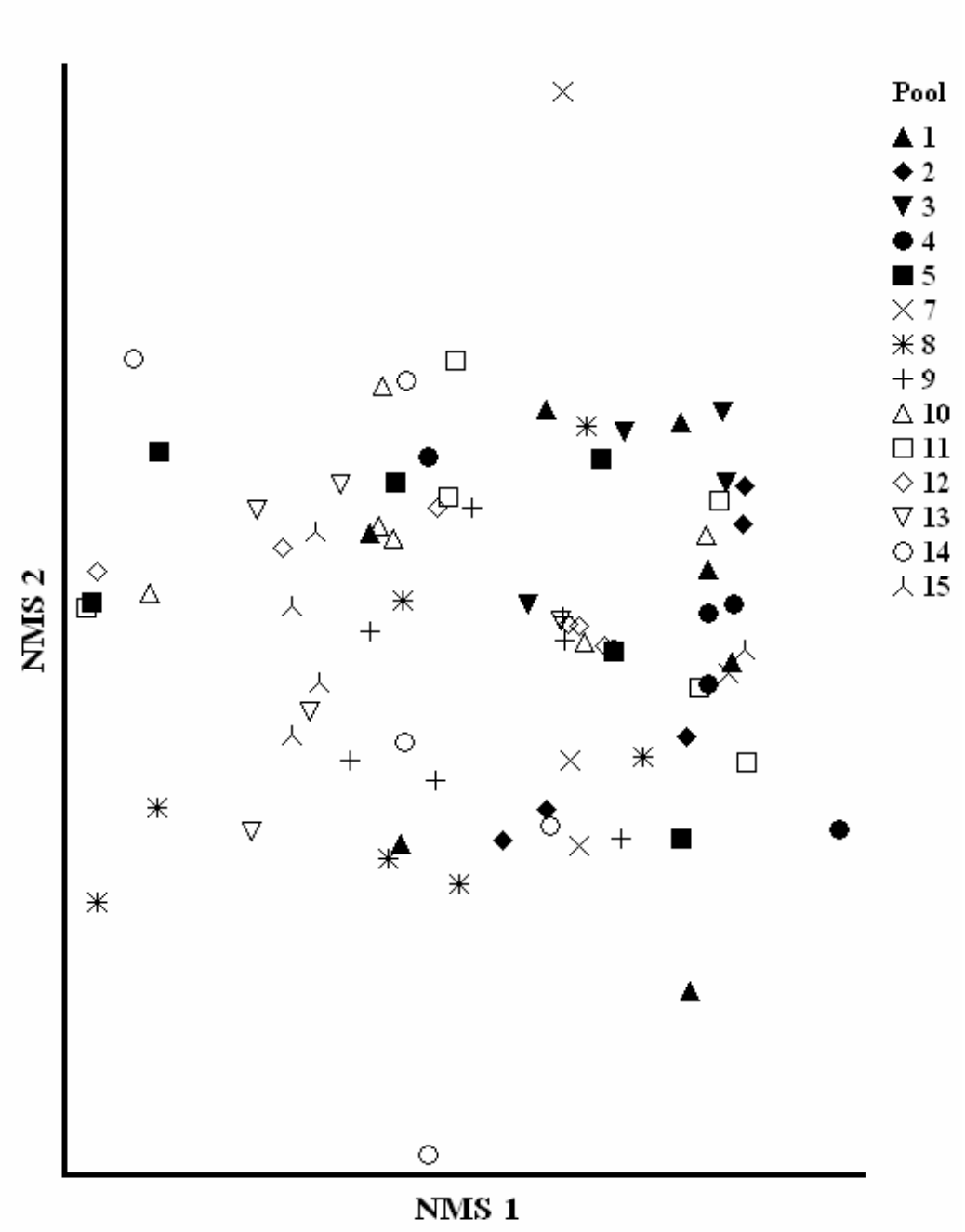

Figure 5. Plot of samples labeled by pool number along the first two axes produced by non-metric multidimensional scaling of fish assemblages of deep pools (n = 79) in the Upper Tombigee River from March 2004 to March 2005.

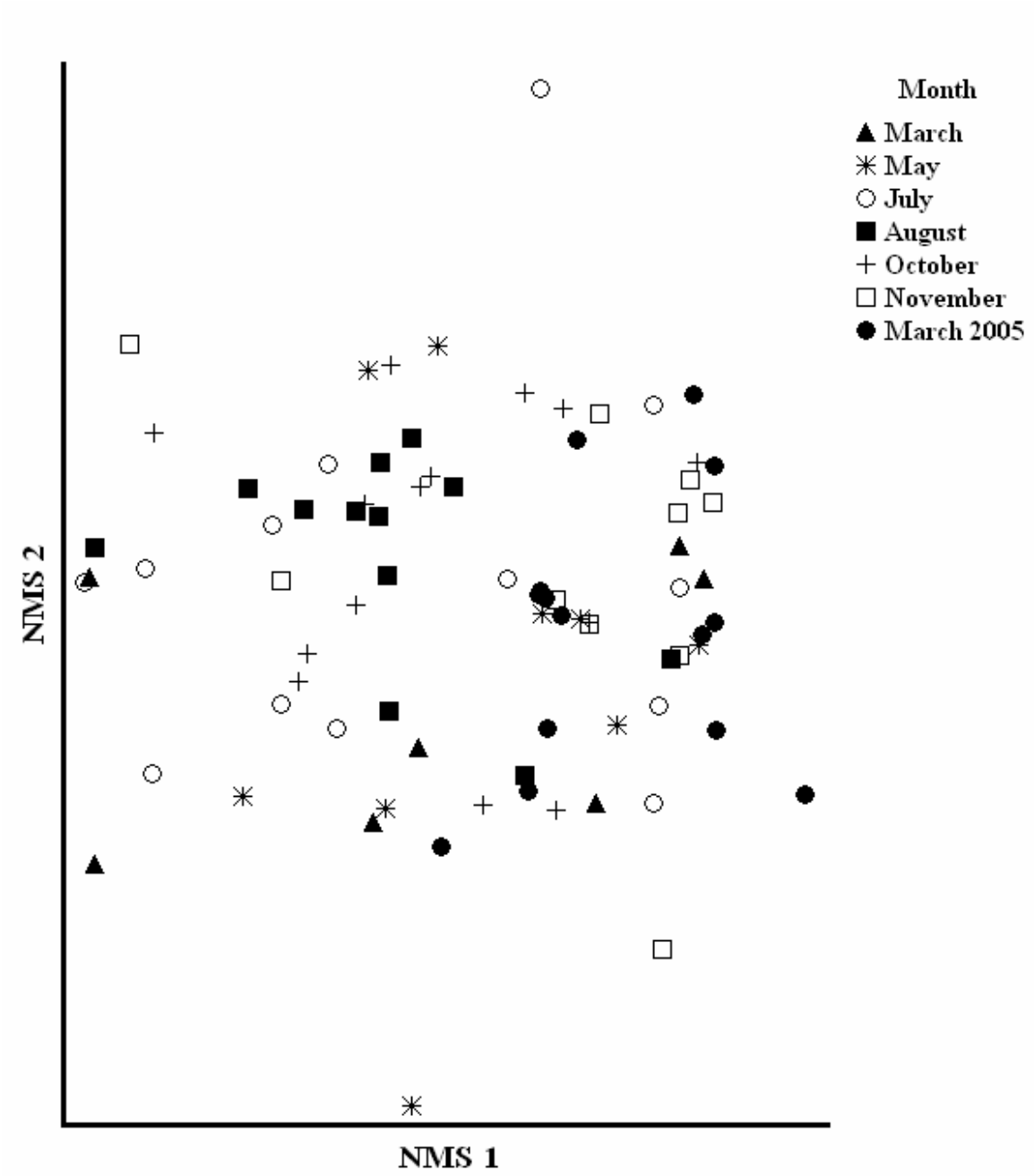

Figure 6. Plot of samples labeled by month of sample along the first two axes produced by non-metric multidimensional scaling of fish assemblages of deep pools (n = 79) in the Upper Tombigee River from March 2004 to March 2005.

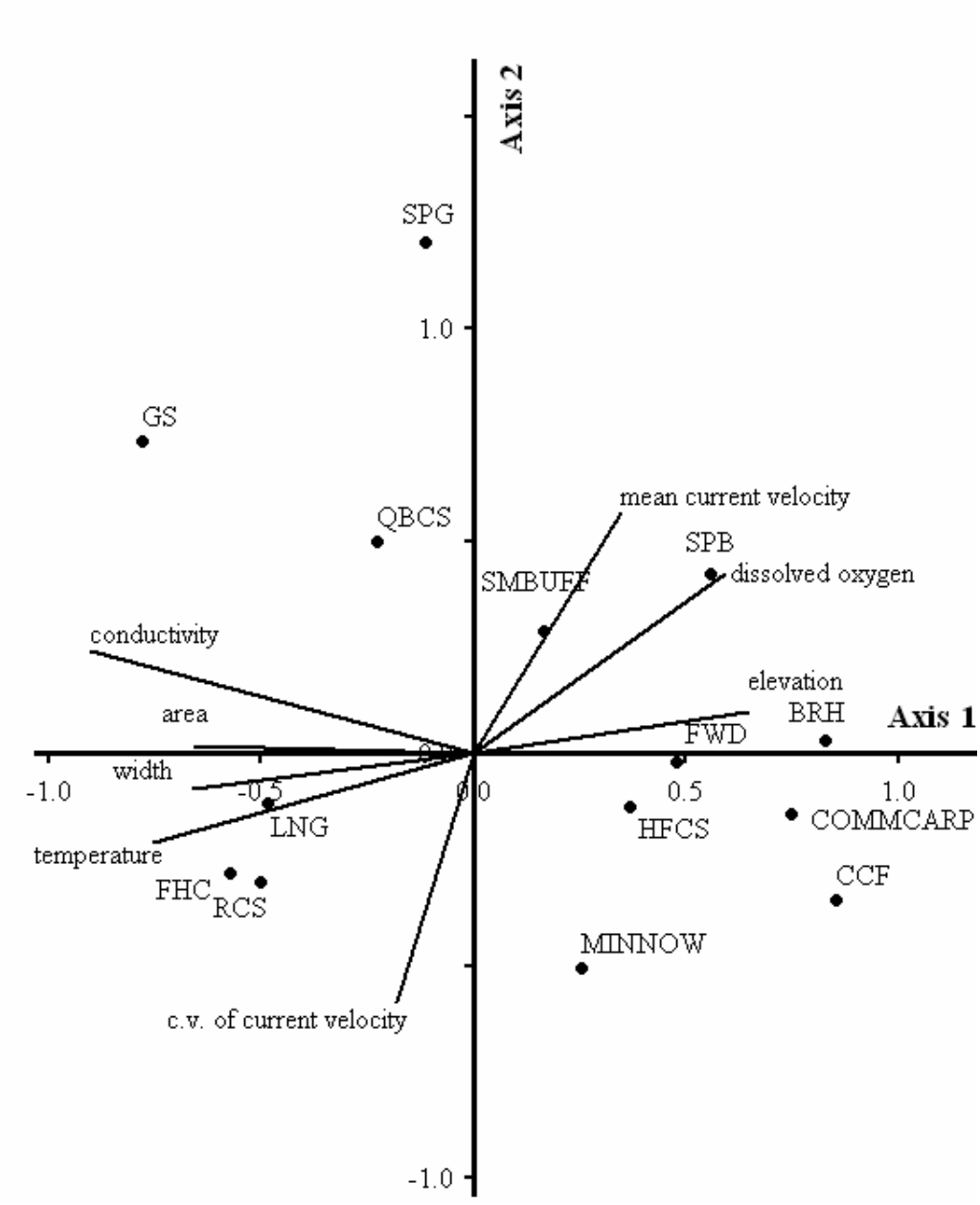

Figure 7. Biplot produced by canonical correspondence analysis of deep pools in the Upper Tombigbee River from March 2004 to March 2005. Vectors indicate the direction and strength of the species-environmental association. (BRH = blacktail redhorse; COMMCARP = common carp; CCF = channel catfish; FHC = flathead catfish; FWD = freshwater drum; GS = gizzard shad; HFCS = highfin carpsucker; LNG = longnose gar; MINNOW = minnow taxonomic group; QBCS = quillback carpsucker; RCS = river carpsucker; SMBUFF = smallmouth buffalo; SPB = spotted bass; SPG = spotted gar.