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[Article]

Assemblage and Population-Level Responses of Stream Fish to Riparian Buffers at Multiple Spatial Scales

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Abstract.—Riparian buffers can improve stream water and habitat quality by reducing non-point-source pollution (e.g., nutrients and sediment), increasing canopy cover and thereby reducing water temperature, and contributing allochthonous organic matter (e.g., leaf litter and woody debris). However, the influence of riparian buffers on biotic assemblages in streams is poorly understood, particularly in the Midwestern United States. In this study, we evaluated the effects of riparian buffers on instream habitat, fish assemblage structure, and population characteristics (i.e., the growth of two small-bodied species) in three streams in central Iowa. The streams were surveyed at two spatial scales; specifically, 41 reaches were sampled and 247 macrohabitat types (i.e., pool, riffle, and run) were subsampled in the summer of 2007. Fish assemblage structure data were summarized into separate data sets by the relative abundance of individual species (i.e., fish per minute of electrofishing) and guilds (e.g., trophic and spawning). Multivariate analysis of variance was used to evaluate the differences in instream habitat and fish assemblage structure between areas with and without riparian buffers. The results indicated little to no relationship between the presence of buffers and fish assemblage structure and instream habitat characteristics. Nonmetric multidimensional scaling (NMS) was used to evaluate the patterns of fish assemblage structure for the reaches and macrohabitat types. The NMS further illustrated the similarity in fish assemblages between buffered and unbuffered reaches. However, the growth of central stonerollers *Campostoma anomalum* was greatest in unbuffered reaches, while that of creek chub *Semotilus atromaculatus* was greatest in buffered reaches. Differences in food availability associated with riparian buffers (e.g., increased algal production and decreased terrestrial invertebrate contributions in unbuffered reaches) probably resulted in growth disparities. The results of this study suggest that while riparian buffers have minimal local effects on instream habitat and fish assemblage structure in Iowa streams, they influence instream features (e.g., food availability) that affect fish population dynamics.

Stream ecosystem integrity has been drastically altered by human disturbances, such as large-scale land use changes, stream channelization, riparian vegetation removal, and destruction of wetlands. According to the National Water Quality Inventory, 44% of rivers and streams in the U.S.A. are considered impaired (EPA 2006). Factors associated with agricultural practices contribute to 27% of all impaired rivers and streams, specific causes of degradation being identified as sediment and nutrient inputs, and habitat alterations that include loss of riparian vegetation (EPA 2006). Land use changes in the Midwestern United States have been more dramatic than other regions of North America. For instance, anthropogenic disturbances in the Great Plains have resulted in losses in area of native terrestrial vegetation as high as 99.9% in the states of Indiana, Illinois, and Iowa (Sampson and Knopf 1994). Replacement of native vegetation with row crops and pasture often has extensive deleterious effects on aquatic ecosystems. Specifically, agricultural practices near streams (i.e., row crops, livestock grazing) reduce streambank vegetation and increase the amount of sediment and nutrients entering streams (Kemp and Dodds 2001). Recognizing consequences of agriculture on water quality in streams and rivers, management agencies are increasingly using conservation practices, such as riparian buffers, to reduce nutrient and sediment inputs to streams (Peterjohn and Correl 1984; Rabeni and Smale 1995; Naiman and Décamps 1997).

Riparian zones play an essential ecosystem role in the physical and biological structuring of streams (Gregory et al. 1991; Naiman and Décamps 1997). As such, the use of riparian buffers to mediate the effects of disturbances on water quality is particularly important because riparian zones are the interface between terrestrial and aquatic ecosystems. Therefore, riparian buffers have been installed and managed most extensively in areas where increases in sedimentation, nutrients, and water temperatures negatively influence fish assemblages throughout North America. It has been demonstrated that vegetated riparian zones (i.e.,

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forested, natural prairie) improve habitat and water quality in coldwater streams of forested regions as well as warmwater systems of the predominantly agricultural Midwest (see Gregory et al. 1991; Osborne and Kovacic 1993; Naiman and Décamps 1997; Sovell et al. 2000). Vegetated riparian zones improve habitat and water quality in streams by reducing sediment and nutrient inputs associated with soil and streambank erosion and fertilizer applications. As such, riparian buffers reduce eutrophication and preserve the integrity of streambed substrate, consequently maintaining and enhancing biotic integrity (Karr and Schlosser 1978; Osborne and Kovacic 1993; Rabeni and Smale 1995; Dodds and Oakes 2006).

Relationships between fish assemblage structure and habitat features in warmwater streams has long been used to quantify disturbance to aquatic ecosystems (Karr 1981) and to understand effects of riparian management practices (Baltz and Moyle 1984; Sovell et al. 2000; Nerbonne and Vondracek 2001; Wang et al. 2006). The relationship between biotic assemblages and land use is often complex because land use can affect stream conditions and processes at multiple spatial scales. Several studies evaluating fish assemblage relationships to land use have demonstrated contradicting results as to the importance of watershed- versus riparian-level influences. In predominately agricultural and urban watersheds, fish assemblage structure is often strongly associated with watershed-scale land use (Roth et al. 1996; Allan et al. 1997; Wang et al. 1997; Roy et al. 2007). This suggests a disproportional influence of highly modified landscapes on stream ecosystems.

Most studies assess riparian conditions across large spatial scales (e.g., Allan et al. 1997; Wang et al. 1997). Stauffer et al. (2000) found that segment-level riparian conditions more strongly influenced fish assemblages than watershed-scale factors in the Minnesota River basin. Similarly, Lammert and Allan (1999) found that reach riparian characteristics better predicted metrics of biotic condition than watershed scale predictors, but that fish and macroinvertebrate assemblages were most closely related to local habitat conditions. A combination of watershed-, reach-, and instream-scale influences explained variation in fish assemblage structure in Michigan streams (Moerke and Lamberti 2006). Due to the complex, multiple-scale influences that structure biotic assemblages and physical habitat in stream ecosystems, the scale at which responses to riparian management are evaluated must be considered due to spatial lags and indirect effects that may confound attempts to understand the structure of assemblages (e.g., Wiens 1989). Moreover, despite the fact that stream fish often require a diversity of habitats to complete their life cycles, many studies fail to address riparian influences at multiple scales in streams. This further emphasizes the need to address fish and habitat relationships at multiple spatial scales.

In addition to fish assemblage characteristics, population characteristics (e.g., age and growth, mortality, recruitment variation) of fish can reflect environmental conditions (e.g., Putman et al. 1995; Shephard and Jackson 2006). Most studies of fish growth have been conducted on sport fishes (e.g., Quist et al. 2003; Paukert and Makinster 2009) or large-bodied species of conservation concern (e.g., Brouder 2005; Eitzmann et al. 2007). Studies focused on growth of small-bodied fishes are uncommon due to the intensive labor and high cost associated with collecting incremental growth data from hard structures (DeVries and Frie 1996). Quist and Guy (2001) examined growth of creek chub *Semotilus atromaculatus*, red shiners *Cyprinella lutrensis*, and green sunfish *Lepomis cyanellus* in Kansas streams. The authors found that growth of all species was positively related to the abundance of woody debris. Therefore, relationships between instream habitat and growth of stream fishes may provide insight into habitat quality because growth integrates and reflects all abiotic and biotic factors (e.g., habitat and food availability) operating over an extensive temporal scale.

The goal of this study was to evaluate the effects of managed riparian buffers on stream fish assemblage characteristics and population dynamics at two in-stream spatial scales (i.e., macrohabitat and reach; Frissel et al. 1986). Specifically, the objectives were to evaluate (1) relationships between physical habitat features and riparian buffer characteristics, (2) potential effects of riparian buffers on taxonomic and functional (i.e., guild) fish assemblage structure, and (3) functional response (i.e., growth) of two ecologically important fish species (i.e., creek chub and central stoneroller *Campostoma anomalum*) to buffered and unbuffered reaches in Midwestern streams.

We hypothesized that relationships of physical habitat and fish assemblage structure to riparian buffers would be more distinguishable at finer (e.g., macrohabitat) spatial scales because possible sources of variation unaccounted for at the larger scales may limit the ability to detect differences in stream habitat and assemblage structure (Frissel et al. 1986). Similarly, we hypothesized that growth of creek chub and central stonerollers would provide better responses than entire assemblages to riparian buffer management practices because growth information allows an assessment of multiple factors limiting populations, including those not directly measured.

Methods

Study sites.—Fish and physical habitat were characterized from 41 reaches and 247 macrohabitats (June–August 2007) in three stream systems: Bear Creek, Long Dick Creek, and Keigley Branch Creek in central Iowa, USA. The Bear Creek watershed is 69.4 km^2, over 87% of the watershed area being used for row crop and pasture agriculture (Isenhart et al. 1997). Bear Creek received extensive riparian habitat enhancement beginning in 1990, including plantings of multispecies riparian buffers along more than 23 km of stream (Isenhart et al. 1997). Schultz et al. (1995) described the design of multispecies riparian buffers established along Bear Creek, which consisted of a tree zone (e.g., five rows of trees planted parallel to the stream), a shrub zone (e.g., two rows of shrubs planted upslope of the tree zone), and a grass zone (e.g., approximately 7-m-wide grass strip planted upslope of the shrub zone). Additional information on the study area and Bear Creek watershed restoration is detailed in Isenhart et al. (1997). The adjacent watershed area and land use of Long Dick Creek and Keigley Branch Creek are nearly identical to Bear Creek but have not yet been the focus of extensive riparian management practices. In addition to having similar land uses, soil types, and climate, the streams have similar connectivity to potential source populations of fishes (i.e., South Skunk River). Habitat and fish assemblages were sampled from 20 reaches in Bear Creek (13 buffered, 7 nonbuffered), 11 reaches from Long Dick Creek (1 buffered, 10 nonbuffered), and 10 reaches from Keigley Branch Creek (3 buffered, 7 nonbuffered).

Reaches were selected from buffered and unbuffered areas from all three streams. Buffered reaches were defined as those that have received targeted riparian improvement activities, and unbuffered reaches were those that lacked active riparian management. Though limited, natural riparian buffers were present in all three watersheds; these areas were avoided to ensure that managed buffers could be compared with similar reaches not receiving conservation practices. In addition to selecting reaches that have received targeted riparian improvement activities, the dominant vegetation-class and land use were assessed at set distance intervals for each reach to ensure that riparian characteristics of buffered and unbuffered reaches were dissimilar. Dominant vegetation-classes included grass, tree or shrub, alfalfa, and corn or soybean; whereas, dominant land use-classes included managed buffer, managed prairie, grass or pasture, and row crop. Vegetation- and land use-classes were visually estimated at 0 (bank), 0–10, 10–30, 30–50, 50–100, 100–250, and 250–500 m. Estimates were conducted at the midpoint of each reach on the left and right bank for all reaches. The percentage of each vegetation- and land use-class was calculated for buffered and unbuffered reaches separately (Figure 1). Unbuffered reaches had corn or soybean as the dominant vegetation-class in 20% of the 0-m (bank) estimates, 33% of the 0–10-m estimates, and 50% of the 10–30-m estimates. Corn or soybeans were absent from 0 to 30 m for buffered reaches (Figure 1).

Fish sampling.—Fish were sampled using a Smith-Root Model LR-20 backpack-mounted DC electrofisher (Smith-Root, Inc., Vancouver, Washington) with two netters in a single upstream pass. Reach length was 35 times the mean stream width (Lyons 1992a; Simonson et al. 1994) or a minimum of 300 m. Macrohabitats in reaches were sampled individually. Prior to sampling and when flows permitted, block nets were set to prevent movement of fishes among sampled macrohabitats. Fish were identified to species and measured to the nearest millimeter (total length), numbers of individuals were counted, and fish were then released in the field. Specimens that could not be identified in the field were preserved in a 10% solution of formalin and transported to the laboratory for identification.

Fish assemblage data were separated into two data sets (taxonomic and functional) to investigate relationships between fish assemblage structure and riparian buffer characteristics. The taxonomic structure data set consisted of relative abundance of species (number of individuals per minute of electrofishing). Species occurring at less than 5% of reaches were excluded from reach analyses, while species occurring at less than 5% of each macrohabitat type were excluded from macrohabitat analyses. Functional groups (e.g., trophic, spawning) often respond more strongly to disturbances (e.g., sedimentation) than common assemblage structural indices (e.g., species richness; Rabeni and Smale 1995). Functional group characteristics used to characterize fish assemblages in stream reaches and macrohabitats included trophic guilds, tolerance to poor habitat and water quality, and richness of different fish taxa. Specifically, functional group variables included richness (of minnows [i.e., Cyprinidae, excluding common carp *Cyprinus carpio*]; darters [i.e., *Etheostoma* spp.]; catfish *Ameiurus*, *Ictalurus*, and *Noturus* spp.; and suckers *Carpiodes, Catostomus*, *Hypentelium*, and *Moxostoma* spp.), intolerant species richness, benthic invertivore richness, proportion of tolerant individuals, proportion of lithophilic spawners, proportion of generalists, proportion of herbivores, proportion of invertivores, and proportion of omnivores. Trophic and tolerance guilds followed those developed for warmwater streams in the Midwest used

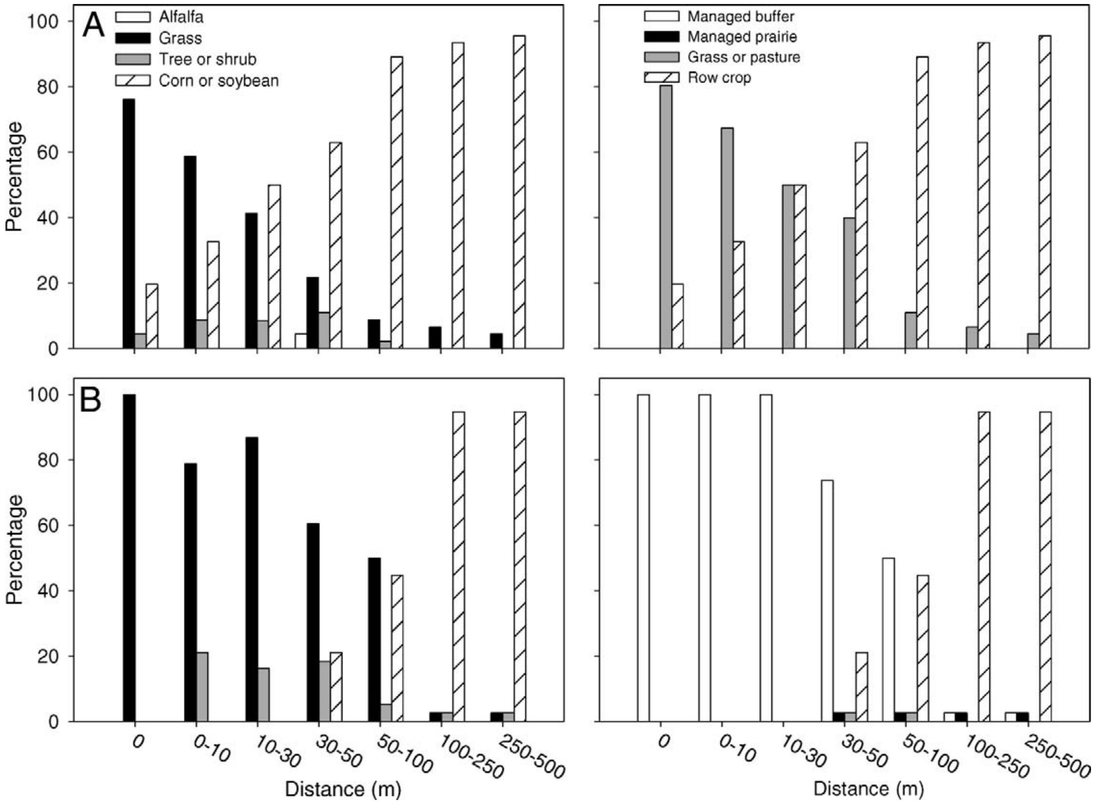

FIGURE 1.—Percentages of vegetation (left panels) and land use classes (right panels) for **(A)** unbuffered and **(B)** buffered reaches at various distances from the streambank in central Iowa, 2007.

to characterize stream fish assemblages (e.g., Karr et al. 1986; Lyons 1992b). Additionally, relative abundance (number of individuals per minute of electrofishing), assemblage evenness, and Shannon's diversity index (Krebs 1999) were calculated to further describe functional assemblage structure in reaches and macrohabitats. Fish assemblage data were summarized separately by reach and macrohabitat.

Differences between buffered and unbuffered stream reaches were also evaluated by examining fish growth in study streams. Fish species evaluated for age and growth analysis were selected to represent different functional feeding-groups that might be expected to respond differently to riparian vegetation management practices. Specifically, central stoneroller is predominately a benthic herbivore and creek chub is a trophic generalist (Pflieger 1997). Otoliths (i.e., asterisci) were removed from 10 fish/cm length-group of each species in all reaches. Otoliths were mounted on glass slides with thermoplastic cement and read under a compound microscope by a single reader to assign ages to individual fish. An age–length key was used to assign ages to lengths of nonaged fish in reaches using methods detailed by Isermann and Knight (2005). Mean length at age (i.e., at capture) was estimated for each species by reach.

Physical habitat.—Physical habitat measurements in macrohabitats were conducted using a transect-based survey method (Simonson et al. 1994). Stream wetted width, depth, bank characteristics, and canopy cover were measured at three equidistant transects (0.25, 0.50, and 0.75 times the total length of macrohabitats). Substrate particle size and depth were measured at four equidistant points and the midpoint (0.2, 0.4, 0.5, 0.6, and 0.8 times the wetted width) along each transect. Substrate was classified using a modified Wentworth scale (i.e., boulder, cobble, gravel, sand, silt, and clay; Cummins 1962). Canopy cover was measured with four readings using a spherical, concave densiometer at the stream banks (facing the streambank), and upstream and downstream of the midpoint at each transect. Aerial coverage of erosional area, vegetation, bare ground, rip-rap, rootwad complex, grass, shrub, and trees was visually estimated at each bank for all

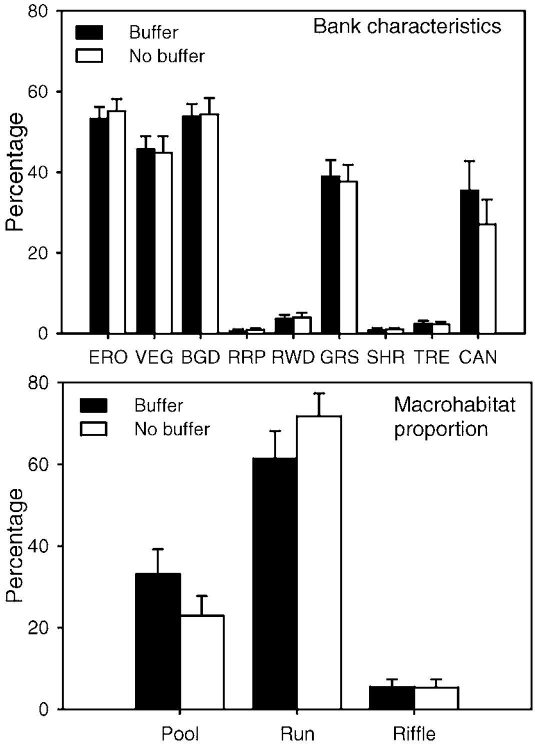

FIGURE 2.—Bank characteristics and proportions of macrohabitats for buffered and unbuffered reaches of streams in central Iowa, 2007. Abbreviations are as follows: ERO = erosion, VEG = vegetation, BGD = bare ground, RRP = riprap (bank), RWD = rootwad, GRS = grasses, SHR = shrubs, TRE = trees, and CAN = canopy cover. Bars represent means + SEs.

transects and averaged for the entire macrohabitat. Within each macrohabitat, area of each instream cover-class was measured (length and width) and summed for instream cover-classes. Instream cover was defined as aquatic vegetation, overhanging vegetation, large woody debris, and rip-rap that was at least 0.3 m long, 0.3 m wide, in water at least 0.3 m deep. Mean physical habitat variables were weighted by macrohabitat length to estimate reach scale values.

Statistical analysis.—Multiple analysis of variance (MANOVA) was used to determine whether physical habitat differed between buffered and unbuffered stream reaches and macrohabitats (Johnson 1998). If MANOVA results were significant, then individual one-way ANOVA was used to determine how variables differed between reaches and macrohabitats with different buffer characteristics. All physical habitat variables (see earlier section) were included as dependent variables in the MANOVA for reach-scale comparisons. Bank characteristics and proportion of macrohabitat area were excluded from macrohabitat-scale comparisons with the MANOVA.

Nonmetric multidimensional scaling (NMS) was used to identify patterns in fish assemblage structure at reach and macrohabitat scales. The NMS was based on Bray–Curtis distance matrices of fish assemblage data. After ordination, a multiresponse permutation procedure (MRPP), using the same distance measure as the NMS, was used to evaluate differences in fish assemblage structure between reaches and macrohabitats with and without riparian buffers (McCune and Grace 2002). The MRPP is a nonparametric procedure that tests the null hypothesis of no difference between two or more groups of assemblages and produces two statistics: a P-value and an A-statistic. The A-statistic measures the effect size of group heterogeneity compared with that by chance (e.g., an A-statistic equal to one indicates assemblages in both groups are identical; McCune and Grace 2002). Indicator species analysis was then used to evaluate differences in taxonomic assemblage structure when results for the MRPP were significant ($P < 0.05$). Indicator species analysis evaluates contributions of individual species to differences between designated groups (i.e., assemblages within buffered and unbuffered reaches and macrohabitats; McCune and Grace 2002). Differences in functional fish assemblage structure between buffered and unbuffered reaches were evaluated using a MANOVA. If the overall MANOVA was significant, individual one-way ANOVAs were used to determine differences between assemblage structure metrics. Strength of correlation between physical habitat and fish assemblage structure was evaluated by calculating Pearson's correlation coefficients of mean physical habitat variables with the sample scores from the NMS ordinations of fish assemblages.

Mean length at age of central stonerollers and creek chub was compared using a Wilcoxon test to evaluate differences between growth in reaches with and without riparian buffers. In addition to mean length at age, growth rates for central stonerollers and creek chub were compared by fitting von Bertalanffy growth models to each population, that is,

$$L_t = L_\infty[1 - e^{-K(t-t_0)}],$$

where L_t is the mean length at age of capture, L_∞ is the theoretical maximum length, K is the growth coefficient, and t_0 is the theoretical age when length equals 0 mm. Growth models were fit to L_t data using nonlinear regression techniques (Freund and Littell 1991). Because K varies with L_∞ (Ricker 1975), K was estimated using a von Bertalanffy growth model with a

TABLE 1.—Mean and SE of functional assemblage structure metrics used to characterize fish assemblages in stream reaches with different buffer types in central Iowa streams, 2007.

	All reaches		Buffered		Nonbuffered	
Variable	Mean	SE	Mean	SE	Mean	SE
Fish abundance (individuals/min)	6.3	0.9	5.3	1.0	7.2	1.3
Number of minnow species	6.3	0.3	5.7	0.5	6.8	0.3
Number of darter species	1.1	0.1	1.1	0.1	1.2	0.1
Number of catfish species	1.3	0.2	1.2	0.2	1.5	0.2
Number of sucker species	1.4	0.1	1.2	0.2	1.5	0.2
Number of intolerant species	1.9	0.2	1.6	0.3	2.2	0.3
Number of benthic invertivores	2.8	0.3	2.3	0.4	3.3	0.4
Percentage of tolerant individuals	14.3	1.6	15.6	2.5	13.1	2.1
Percentage of lithophilic individuals	68.4	1.9	71.3	3.1	66.0	2.4
Percentage of generalist individuals	32.2	3.2	39.1	5.5	26.3	3.5
Percentage of herbivore individuals	5.7	0.8	4.6	1.0	6.7	1.3
Percentage of invertivore individuals	28.8	1.8	27.9	2.8	29.6	2.4
Percentage of omnivore individuals	32.4	2.3	28.0	4.1	36.3	2.4
Evenness	0.75	0.01	0.72	0.03	0.77	0.02
Shannon's diversity index	1.78	0.07	1.64	0.12	1.90	0.08

fixed L_∞ (i.e., defined as the maximum length of each species collected in the study). The mean growth coefficients of populations from reaches with and without riparian buffers were compared with a Wilcoxon test. Nonmetric multidimensional scaling, multiresponse permutation procedures, and indicator species analyses were conducted using PC-ORD, version 5.0 (McCune and Grace 2002). All other analyses were conducted using SAS 9.1.3 (SAS Institute 2006). A type I error rate of 0.05 was used for all statistical tests.

Results

Physical Habitat

Physical habitat was highly variable among the 41 sampled reaches. Mean width varied from 1.0 to 7.5 m (4.2 ± 0.3 m [overall mean ± SE]) and mean depth varied from 0.12 to 0.48 m (0.29 ± 0.02 m) among reaches. Bank characteristics were also highly variable among reaches. Mean bank vegetation cover varied from 20.1% to 100% (47.0 ± 2.9%), while mean canopy cover varied from 0% to 87.7% (20.9 ± 4.2%). Sand was the most prevalent substrate-class recorded, there being over 25% composition in greater than 80% of the sampled reaches. However, substrate composition among reaches varied from 3.0% to 100% (34.5 ± 3.6%) for silt, followed by 0–78.7% (40.4 ± 2.7%) for sand, 0–43.2% (7.9 ± 1.7%) for cobble, 0–32.9% (14.0 ± 1.5%) for gravel, 0–19.3% for boulder (3.0 ± 0.7%), and 0–3.6% (0.2 ± 0.1%) for clay. Overall, the most abundant form of instream cover was aquatic vegetation (0–86.6% of the instream area within reaches; 8.3 ± 3.5%), followed by large woody debris (0–14.0%; 2.0 ± 0.5%), rip-rap (0–5.7%; 0.6 ± 0.2%), and overhanging vegetation (0–3.6%; 0.4 ± 0.1%). Similarly, physical habitat in macrohabitats varied as pools and runs tended to be deeper and possess finer substrates than riffle habitats that were shallow and dominated by large substrates. Stream size, bank characteristics, substrate composition, and instream cover were similar between reaches and macrohabitats with and without riparian buffers (Figures 2, 3). Physical habitat did not differ between buffered and unbuffered reaches ($\lambda_{20,21} = 0.46$; $P = 0.32$), pools ($\lambda_{11,15} = 0.46$; $P = 0.19$), runs ($\lambda_{11,28} = 0.65$; $P = 0.25$), or riffles ($\lambda_{9,6} = 0.36$; $P = 0.44$).

Fish Assemblages

A total of 27 species and 7,649 fish was collected from 41 sampled reaches in all three streams. Four species (creek chub, bluntnose minnow *Pimephales notatus*, common shiner *Luxilus cornutus*, and white sucker *Catostomas commersonii*) were collected at over 90.2% of the sampled reaches. Species richness varied substantially among reaches (3–18 species), and native species comprised 97.9–100% of the total number of individuals sampled. Cyprinids were the dominant family, comprising over half of the individuals collected in greater than 85% of reaches. In addition, Cyprinidae was the only family collected in all reaches. Generalists were the most common trophic guild sampled, but the proportion of generalists varied considerably (4.3–82.1% of the individuals collected) across reaches. Omnivores comprised 3.6–58.7% of the individuals collected in a reach. Intolerant species were sampled in all reaches, and their proportional contribution to the sampled assemblage varied from 3.2% to 73.5% of the total number of individuals in a reach. Fish assemblage characteristics did not differ between reaches with and without riparian buffers ($\lambda_{15,25} =$

0.53, $P = 0.20$; Table 1). Similarly, no difference in fish assemblage characteristics were found between pools ($\lambda_{15,11} = 0.31$; $P = 0.22$) and runs ($\lambda_{15,24} = 0.61$; $P = 0.45$). A MANOVA was not calculated for fish assemblage characteristics in riffle habitats due to small sample size.

Stable NMS ordinations were obtained for the functional fish assemblage structure for reaches and all macrohabitat types (Figures 4–7). Similarly, the taxonomic structure of fish assemblages resulted in stable NMS ordinations for reaches, pools, and runs (Figures 4–6). A stable NMS ordination for the taxonomic structure of fish assemblages in riffle macrohabitats was not obtained. The NMS ordinations for reaches and run habitats had lower stress for taxonomic assemblage data (6.0% and 10.7%, respectively) than functional assemblage data (8.9% and 12.3%, respectively; Figures 4, 5), suggesting that taxonomic fish assemblage structure maximized the amount of variation explained. Conversely, the NMS ordination of functional structure had lower stress (10.8%) compared with the ordination of taxonomic structure (13.1%) for pool macrohabitats (Figure 6). Stress was lowest for the NMS ordination of riffle functional assemblage data (3.4%; Figure 7) but was likely due to the small sample size relative to the number of functional characteristics included in the fish assemblage data set.

Results from the MRPP indicated that the functional structure of fish assemblage was similar between reaches with and without riparian buffers ($P = 0.078$; $= 0.018$), whereas a difference in taxonomic structure was significant ($P = 0.046$; $A = 0.015$). Black bullhead *Ameiurus melas* and black crappie *Pomoxis nigromaculatus* were significant positive indicators of reaches with riparian buffers (Table 2). No single species was a significant indicator of reaches without riparian buffers. Differences in taxonomic ($P = 0.012$; $A = 0.028$) and functional ($P = 0.038$; $A = 0.034$) assemblage data were observed for pool macrohabitats. Black bullhead and white sucker were significant indicators of pools with riparian buffers, while fantail darter *Etheostoma flabellare* was the only species that was significantly associated with pools in reaches lacking buffers (Table 2). The MRPP results of run and riffle macrohabitats indicated no differences in fish assemblage structure between reaches with and without riparian buffers.

Fish assemblage structure was related to physical habitat at the reach and macrohabitat scales. At the reach scale, functional and taxonomic fish assemblage NMS axis scores were correlated with stream size (depth and width), bank characteristics (vegetation, riprap), substrate composition (proportion silt), instream cover (aquatic vegetation), and proportion of macrohabitat types (pool and run; Table 3). The strongest relationship between functional assemblage structure and physical habitat was stream width (axis 2: $r = -0.53$, $P < 0.01$), followed by stream depth (axis 2: $r = -0.52$, $P < 0.01$). Similarly, taxonomic structure was most strongly related to stream depth (axis 2: $r = 0.62$, $P < 0.01$) and stream width (axis 2: $r = 0.55$, $P < 0.01$). In pool macrohabitats, taxonomic and functional structure of fish assemblages was related to stream size, canopy cover, and aquatic vegetation (Table 4). The strongest relation between habitat and assemblage structure in pool macrohabitats was mean width for functional (axis 2: $r = -0.47$, $P = 0.01$) and taxonomic data sets (axis 2: $r = 0.66$, $P < 0.01$). The functional structure of riffle fish assemblages was only correlated with depth (axis 1: $r = 0.63$, $P = 0.01$). The functional assemblage structure of run macrohabitats was most strongly correlated with the proportion of silt (axis 2: $r = 0.55$, $P < 0.01$), followed by depth (axis 1: $r = -0.50$, $P < 0.01$). Similarly, run taxonomic assemblage structure was most strongly correlated with depth (axis 2: $r = -0.73$, $P < 0.01$), followed by proportion of silt (axis 1: $r = -0.52$, $P < 0.01$) and width (axis 2: $r = -0.52$, $P < 0.01$).

Age and Growth

A total of 466 central stonerollers was collected and 192 structures were aged from all sampled reaches. Ages of central stonerollers varied from 0 to 4 years (Figure 8). Mean length at age for central stonerollers varied from 36 to 52 mm for age 0, 44 to 114 mm for age 1, 70 to 125 mm for age 2, 88 to 130 mm for age 3, and 97 to 122 mm for age 4. Mean lengths at age differed between reaches with and without riparian buffers for age-1 ($W = 6,759.0$; $P = 0.0014$), age-2 ($W = 4,305.0$; $P = 0.0003$), and age-3 ($W = 880.0$; $P = 0.0002$) fish. No age-0 fish were collected in reaches with riparian buffers. Additionally, comparison of mean length of age-4 fish was not conducted since only two age-4 individuals were captured in reaches without buffers. In addition to mean lengths, estimated growth coefficients for central stonerollers in reaches with and without riparian buffers also differed ($W = 153.0$, $P < 0.0001$; Figure 8).

A total of 806 structures was aged from 2,000 creek chub collected in all sampling. The maximum age of creek chub collected was four (Figure 8). Creek chub mean lengths at age varied from 28 to 59 mm for age 0, 41–137 mm for age 1, 63–168 mm for age 2, 100–221 mm for age 3, and 122–238 mm for age 4. The mean length at age of capture for creek chub differed between reaches with and without riparian buffers for age-0 ($W = 842.5$, $P < 0.0001$), age-1 ($W = 71,426.5$, $P < 0.0001$), age-2 ($W = 158,590.5$, $P < 0.0001$), age-

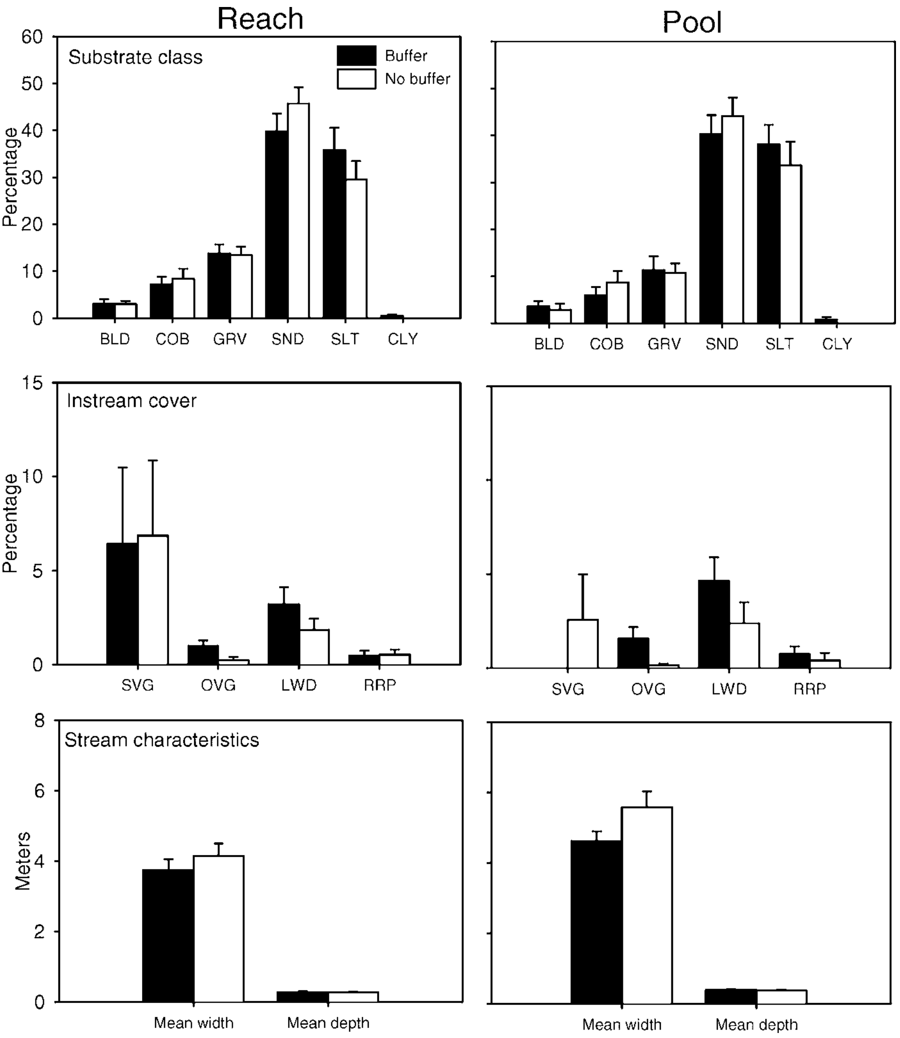

FIGURE 3.—Mean instream physical habitat variables measured in buffered and unbuffered reaches and macrohabitats (pool, run, or riffle) in central Iowa streams, 2007. Abbreviations are as follows: BLD = boulder, COB = cobble, GRV = gravel, SND = sand, SLT = silt, CLY = clay, SVG = aquatic vegetation, OVG = overhanging vegetation, LWD = large woody debris, and RRP = rip-rap (instream). Bars represent means + SEs.

3 ($W = 56{,}248.0$, $P < 0.0001$), and age-4 fish ($W = 1{,}130.5$, $P = 0.0062$). The mean growth coefficients of creek chub populations from reaches with and without riparian buffers were significantly different ($W = 589.0$, $P < 0.0001$; Figure 8).

Discussion

Fish assemblage structure of the study streams was not highly influenced by the presence of riparian buffers but rather related to instream habitat. Factors significantly correlated with NMS axes included characteristics of stream size (e.g., width or depth) and instream cover (e.g., aquatic vegetation) at both the reach and macrohabitat scale. Many previous studies evaluating relative influence of watershed and riparian scale influences determined that instream habitat and assemblage composition were most strongly associated with watershed-scale characteristics (e.g., Roth et al. 1996; Wang et al. 1997; Snyder et al. 2003). Therefore, lack of association between instream features and riparian characteristics may be due to the overwhelming influence of agriculture in the watershed. Wang et al. (1997) found little or no effect of agricultural influence on habitat quality and fish assemblage composition in watersheds with less than 50% agricultural land use, but biotic integrity was substan-

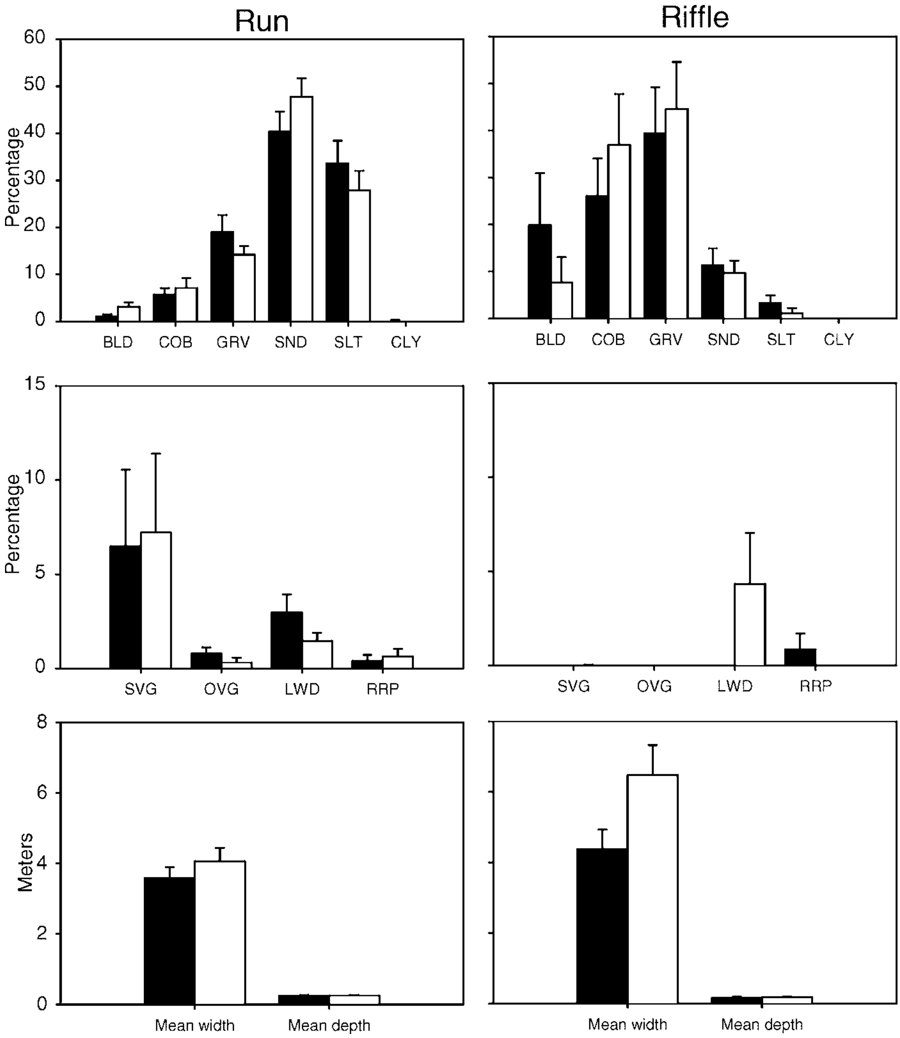

FIGURE 3.—Continued.

tially reduced when agricultural land use exceeded 80%. The prevalence of agricultural land use is extremely high in Iowa, as 81% of land area is influenced by agricultural practices (NRCS 2007). Therefore, conditions in highly altered watersheds may reflect reduced natural variation in environmental conditions, resulting in less power to detect differences. In contrast, Stauffer et al. (2000) found that fish assemblage composition was influenced by local riparian zone conditions in predominately agricultural watersheds (87.7–96.6% agricultural land use) in the Minnesota River basin. Agricultural land use in the watersheds of Bear, Keigley Branch, and Long Dick creeks was similar to that studied by Stauffer et al. (2000), but one notable difference between our studies is that we evaluated effects of artificial riparian buffers on streams, whereas Stauffer et al. (2000) selected streams reaches a priori based on specific riparian zone characteristics to be evaluated. The disproportionally strong influence of watershed land use on stream habitat quality and assemblage composition, coupled with extensive landscape alteration and relatively new (i.e., less than 20-years-old) riparian buffers, may have limited the ability to detect responses of habitat conditions and assemblage structure caused by riparian buffers.

Instream physical habitat has long been acknowledged as one of the most influential factors structuring taxonomic composition and abundance of stream fishes (Gorman and Karr 1978; Schlosser 1982; Angermeier

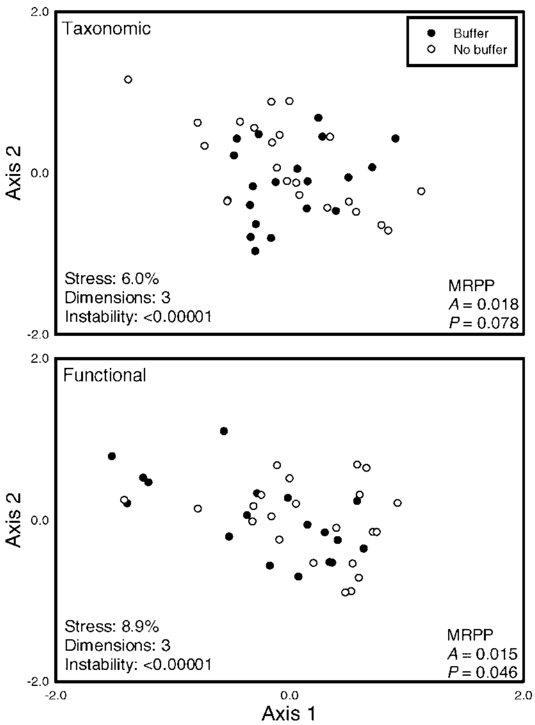

FIGURE 4.—Nonmeric multidimensional scaling for fish assemblage structure (taxonomic and functional) in central Iowa streams, 2007, with A-statistics (a measure of group heterogeneity) and P-values from the multiresponse permutation procedure (MRPP).

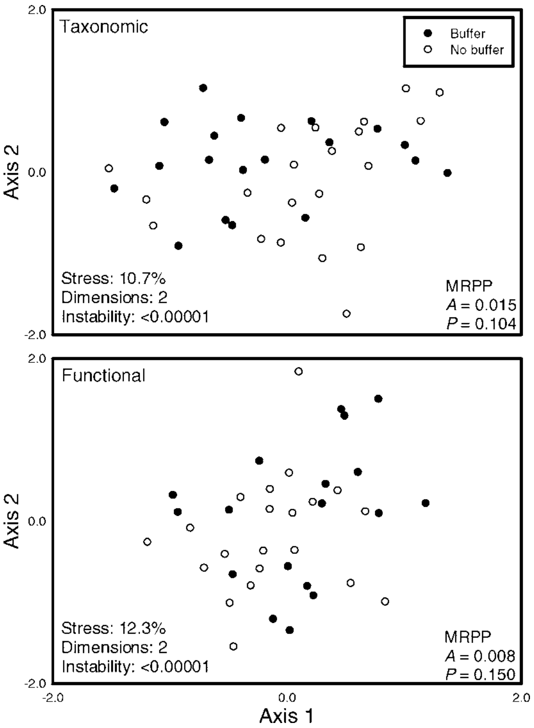

FIGURE 5.—Nonmetric multidimensional scaling for fish assemblage structure in run macrohabitats in central Iowa streams, 2007; see Figure 4 for more details.

and Karr 1984). Additionally, streams are naturally heterogeneous and hierarchically structured, yet many studies do not evaluate habitat and assemblage structure at multiple spatial scales in streams (Frissel et al. 1986; Fausch et al. 2002). Furthermore, results from research evaluating the relative importance of riparian influences on biotic assemblages and instream physicochemical habitat have been mixed. In the River Raisin basin of Michigan, Lammert and Allan (1999) found that riparian characteristics explained greater variation in fish assemblage composition than watershed characteristics, while Roth et al. (1996) found land use at the entire watershed-scale to be a better predictor of fish assemblages than riparian characteristics. Due to the influence of physical habitat (e.g., macrohabitat type) on fish assemblages and a lack of knowledge as to importance of riparian versus watershed influences on stream ecosystems, we evaluated the structure of instream habitat and assemblage composition at reach and macrohabitat scales. By measuring biotic and abiotic relationships with riparian buffers at both reach and macrohabitat scales, we increased the likelihood of detecting potential riparian buffer effects. For example, riffle macrohabitats with greater relative compositions of coarse substrates may be disproportionally impacted by

TABLE 2.—Observed and mean predicted indicator values (IVs) for species sampled in central Iowa, 2007, for which buffer type was significant ($P < 0.05$). The P-values are based on the proportion of 1,000 Monte Carlo randomizations for which IV equaled or exceeded the observed IV.

Scale and species	Buffer type	Observed IV	Mean IV	SD	*P*
Reach					
Black bullhead	Buffered	36.1	21.6	6.6	0.03
Black crappie	Buffered	21.1	9.8	4.3	0.04
Pool					
Black bullhead	Buffered	40.9	22.8	8.0	0.03
White sucker	Buffered	67.4	50.9	6.5	0.02
Fantail darter	Nonbuffered	38.5	17.8	7.0	0.01

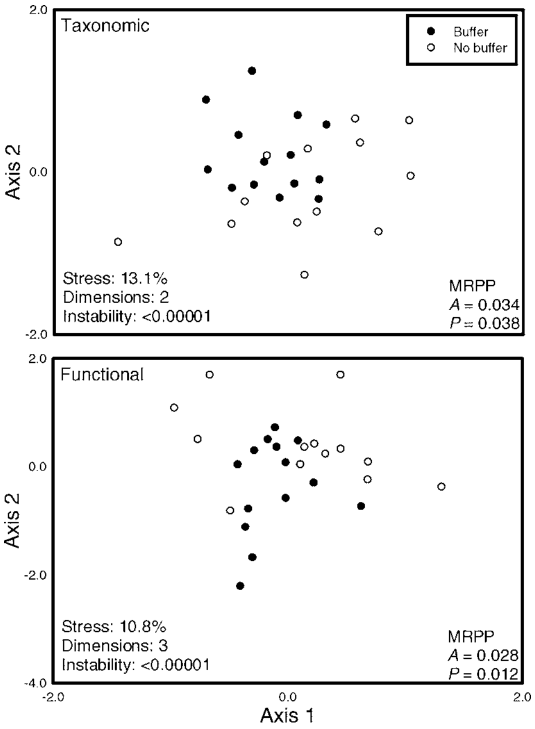

FIGURE 6.—Nonmetric multidimensional scaling for fish assemblage structure in pool macrohabitats in central Iowa streams, 2007; see Figure 4 for more details.

disturbances that increase sediment transport as opposed to pools or other depositional habitats that are typically dominated by fine sediment (Waters 1995). Despite accounting for a variety of habitat scales, we found no biologically meaningful differences between presence and absence of riparian buffers and fish assemblage characteristics.

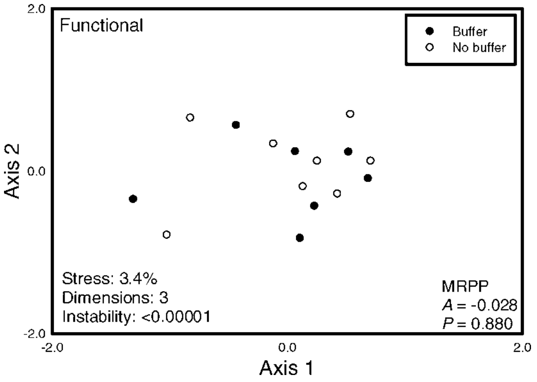

FIGURE 7.—Nonmetric multidimensional scaling for fish assemblage structure in riffle macrohabitats in central Iowa streams, 2007; see Figure 4 for more details.

Fish are considered important ecological indicators of aquatic system health due to their predictable structural response to chemical, physical, and biological disturbances; their socioeconomic and esthetic values; and their relative ease of monitoring compared with other aquatic organisms (Simon 1998). As such, fish assemblages are often used to evaluate effects of riparian conditions on ecosystem function in streams (e.g., Roth et al. 1996; Wang et al. 1997; Lammert and Allan 1999; Snyder et al. 2003). The similarity of fish assemblage structure between reaches with and without riparian buffers may be attributed to the ecology of prairie stream fishes. Prairie stream fishes evolved in systems characterized by high variability in physico-

TABLE 3.—Pearson correlation coefficients (*r*) of nonmetric multidimensional scaling ordination sample scores of instream physical habitat variables for reaches sampled in central Iowa streams, 2007. Only significant correlations are provided.

	Axis 1		Axis 2		Axis 3	
Variable	*r*	*P*	*r*	*P*	*r*	*P*
Taxonomic						
Mean width	−0.38	0.01	0.55	<0.01		
Mean depth	−0.46	<0.01	0.62	<0.01	0.43	<0.01
Mean bank vegetation					0.41	<0.01
Mean silt					0.54	<0.01
Mean aquatic vegetation					0.49	<0.01
Percent pool			0.33	0.04		
Percent run			−0.37	0.02		
Functional						
Mean width	0.40	<0.01	−0.53	<0.01	−0.48	<0.01
Mean depth			−0.52	<0.01		
Mean bank rip-rap			−0.37	0.02		
Mean bank grass					0.32	0.04
Mean silt	−0.51	<0.01	0.37	0.02	0.46	<0.01
Mean aquatic vegetation	−0.36	0.02				
Percent pool			−0.48	<0.01		
Percent run			0.50	<0.01		

TABLE 4.—Pearson correlation coefficients (r) of nonmetric multidimensional scaling ordination sample scores of instream physical habitat variables for macrohabitats sampled in central Iowa streams, 2007. Only significant correlations are provided.

	Axis 1		Axis 2	
Variable	*r*	*P*	*r*	*P*
Pool				
Taxonomic				
Mean width			0.66	<0.01
Mean depth	−0.41	0.03		
Mean aquatic vegetation	−0.42	0.03		
Functional				
Mean width			0.47	0.01
Mean canopy cover	−0.42	0.03		
Riffle				
Functional				
Mean depth	0.63	0.01		
Run				
Taxonomic				
Mean width			−0.52	<0.01
Mean depth	−0.49	<0.01	−0.73	<0.01
Mean silt	−0.52	<0.01		
Mean aquatic vegetation	−0.47	<0.01		
Functional				
Mean width	−0.36	0.02	−0.42	<0.01
Mean depth	−0.50	<0.01		
Mean silt			0.55	<0.01
Mean aquatic vegetation			0.35	0.03

chemical habitat characteristics such as elevated sediment delivery and extremes in thermal and discharge characteristics (Fausch and Bestgen 1997; Dodds et al. 2004). Innate tolerance to perturbations in physical habitat may make it difficult to detect response to anthropogenic disturbances. Therefore, the use of fish assemblages to measure responses caused by restoration efforts may be limited by the extent, intensity, and duration of disturbances being mediated. Although assemblage structure varied substantially among reaches (e.g., 3.2–73.5% of individuals classified as tolerant), almost all individuals (i.e., 97.9–100%) were native species that are thought to be adapted to the extreme physicochemical conditions characteristic of the Great Plains (Fausch and Bestgen 1997).

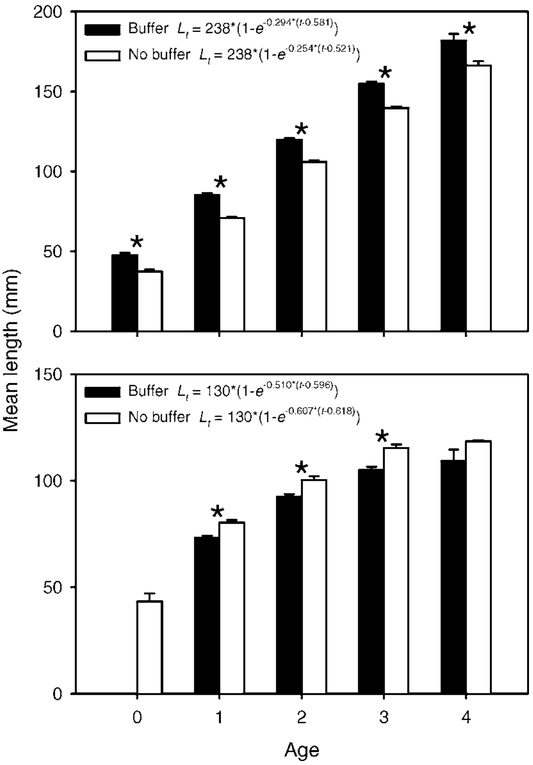

FIGURE 8.—Mean length at age for creek chub (upper panel) and central stonerollers (lower panel) collected from reaches with and without riparian buffers in central Iowa streams, 2007. Bars represent means + SEs, and asterisks indicate significant differences ($P < 0.05$) according to a Wilcoxon test. The equations are the best-fit von Bertalanffy growth models.

Although prairie stream fishes are adapted to harsh environmental conditions, intensive widespread disturbance to the Great Plains for over a century may overshadow recent improvements in riparian habitat quality. For instance, destruction of instream habitat, including physical refuges, as a result of long-term sedimentation may have eliminated many intolerant species from ecosystems. Therefore, source populations are unavailable to repopulate available habitats after they are restored. The "ghost of disturbance past" hypothesis proposed by Harding et al. (1998) describes how current fish assemblages may represent a reduced species pool due to lack of undisturbed habitat fragments large enough to support populations of more-sensitive species. A study of historical fish assemblage trends of the Little Sioux River basin in northwestern Iowa found no change in the number of species or their tolerances to environmental degradation from 1932 to 2002 despite major improvements in land use stewardship (Palić et al. 2007). The recent fish assemblage of the Little Sioux River basin was dominated by species (e.g., creek chub, sand shiner *Notropis stramineus*, and common carp *Cyprinus carpio*) at least moderately tolerant of habitat degradation (Palić et al. 2007). Similar findings have been documented throughout the Midwest in Kansas (Cross and Moss 1987), Oklahoma (Rutherford et al. 1987), and Illinois (Larimore and Bayley 1996). Furthermore, most early collections of stream fish in the Midwest occurred after widespread anthropogenic disturbances caused by agriculture, leaving presettlement conditions poorly documented (Matthews 1988; Fausch and Bestgen 1997). As such, even the earliest documented fish occurrences may reflect substantially reduced species pools that have changed little since they were first sampled. Thus, even after substantial improvements to aquatic habitat, fish assemblages may not reflect improved water quality conditions without reintroduction efforts.

The widespread use of subsurface drainage tile throughout Iowa and much of the Midwest may have also reduced the ability to detect differences between buffered and unbuffered reaches. Installation of drainage tile is a common practice in the Midwest, resulting in increased area for agricultural production. For example, the use of drainage tile resulted in an increase in the percentage of cultivated land in the study area (i.e., Story County) from 40% in 1884 to 75% by 1947 (Hewes and Frandson 1952). Surface runoff to streams and rivers is decreased, while drain tiles transport water, nutrients, sediment, and agricultural chemicals directly from uplands to rivers and streams (Jaynes et al. 2001; Kalita et al. 2006; Schilling and Helmers 2008). Because drainage tiles create direct pathways for runoff to enter streams, the function of riparian buffers is likely diminished. As such, the observed lack of differences between buffered and unbuffered stream characteristics and fish assemblages may be due to the presence of drainage tile. Despite its widespread use, most drainage tile was installed prior 1920, and sparse documentation of drainage tile lines is available (Hewes and Frandson 1952). Although drainage tile may reduce the potential of riparian buffers to mediate the effects of agriculture in the watershed, naturally vegetated riparian zones still provide sources of allochthonous organic matter, limit streambank erosion, and provide protection from solar irradiance.

In the current study, presence of riparian buffers had little or no effect on instream physical habitat and fish assemblage structure. Although differences were observed in fish assemblage structure in reaches and pool macrohabitats, riparian buffers were primarily associated with greater abundances of black bullhead (a tolerant, habitat generalist; Pflieger 1997). However, clear functional responses (i.e., fish growth) to riparian buffers were observed. Specifically, growth of central stonerollers was fastest in unbuffered reaches, while growth of creek chub was fastest in buffered reaches. Exact mechanisms for significant relationships between riparian features and fish growth are unknown.

The conflicting growth response of the two species to riparian buffers was likely due to their differing ecological requirements. Both central stonerollers and creek chub exhibit habitat and diet characteristics that may be expected to respond to riparian buffers. Central stonerollers are habitat generalists commonly found in pools, runs, and riffles. Although central stonerollers often consume aquatic macroinvertebrates, they are typically considered an herbivore given that their diet is dominated by algae and other plant material (Pflieger 1997; Evans-White et al. 2003). Growth of central stonerollers in the current study was highest in unbuffered reaches. Unbuffered stream reaches tended to be wide and have low canopy coverage and low overhanging vegetation. Increased riparian vegetation and canopy cover can decrease algal biomass through reduction of solar energy and allochthonous nutrient inputs (e.g., leaf litter), which can indirectly decrease abundance and diversity of herbivorous macroinvertebrates (DeNicola and Hoagland 1996; Quinn et al. 1997). The lack of riparian vegetation in unbuffered reaches of this study may have contributed to increased autochthonus production through greater solar irradiance or nutrient loads from the unbuffered riparian areas (Isenhart et al. 1997). Therefore, fast growth of central stonerollers is likely a response to increased quantity and quality of food resources as a result of enhanced autochthonous production in stream reaches without buffers.

In contrast to central stonerollers, creek chub exhibited faster growth in buffered stream reaches compared with those without riparian buffers. Creek chub are habitat generalists and are often associated with pools of small streams and instream cover (e.g., aquatic vegetation, woody debris; McMahon 1982; Hubert and Rahel 1989; Quist and Guy 2001). Additionally, adult creek chub are trophic generalists that feed on aquatic and terrestrial invertebrates as well as fishes (Dinsmore 1962; Quist et al. 2006). Juveniles often feed predominantly on aquatic invertebrates (Magnan and FitzGerald 1984). Although not statistically significant, buffered stream reaches tended to have more woody debris, overhanging vegetation, and canopy coverage than unbuffered reaches. Increased instream cover in buffered reaches may have provided more suitable habitat for juvenile and adult creek chub, resulting in increased growth. Woody debris can increase the abundance and diversity of aquatic invertebrates in streams as well as provide fish with refuge from predators and high current velocities (Angermeier and Karr 1984; Benke et al. 1984). Additionally, riparian vegetation can increase the abundance and availability of terrestrial invertebrates, consequently contributing to the diet of insectivorous fishes (Cadwallader et al. 1980; Allan et al. 2003; Baxter et al. 2005). Thus, increased growth of creek chub is likely due to a combination of increased prey resources associated with woody debris and terrestrial production, coupled with increased habitat complexity as a result of greater instream cover.

Although we did not observe differences in fish assemblage structure associated with riparian buffers, we observed functional responses (i.e., growth) of two important Great Plains fishes. Few studies have evaluated incremental growth of small-bodied stream fishes, and no previous studies, to our knowledge, have related growth of fish in small streams to riparian characteristics. Results of this study illustrate the importance of incorporating information on population dynamics with traditional measures of biological monitoring (e.g., assemblage structure) to fully understand the complex relationships between fish and their habitat. Further studies addressing the influence of riparian buffers on the availability and utilization of food resources (i.e., benthic primary production, terrestrial invertebrate contributions to stream systems) for fishes are needed to identify the mechanisms responsible for the observed differences in fish growth.

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