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Relationships between fish assemblages and habitat characteristics in Iowa's non-wadeable rivers

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Abstract Non-wadeable river systems are some of the most diverse aquatic ecosystems, but little work has been conducted to quantify the relationships between fish assemblages and habitat characteristics in them. In 2007 and 2008, 21 reaches were sampled on 16 non-wadeable rivers across Iowa, USA. Fish were sampled in each reach with three different gears, and habitat characteristics (channel morphology, current velocity, instream cover) were measured using standard procedures. Fish assemblages were structured based on drainage basin and reaches and could be categorised as belonging to one of three groups. Reaches in the Missouri River basin group were narrow and had a high proportion of fine substrate. Reaches in the Mississippi River A group were also narrow but had a high proportion of large rocky substrate. Reaches in the Mississippi River B group tended to be wider, deeper and have higher proportions of fine substrate than the other groups. Fish assemblages were closely related to habitat characteristics and reflected differences among the three groups. Results of this study suggest that stream geomorphology may have a substantial influence on fish assemblage structure in large rivers.

KEYWORDS: agriculture, fish assemblage structure, non-metric multidimensional scaling, stream geomorphology.

Introduction

North America is considered to have the greatest temperate freshwater biodiversity of all the continents (Abell *et al*. 2000), but many freshwater taxa are impaired (Master 1990). Freshwater fishes are one of the most impaired taxa, with 35% of species listed as imperilled or extinct; 27 species of freshwater fish in North America have gone extinct in the last 100 years (Miller *et al*. 1989). By comparison, only 14% of terrestrial vertebrates (e.g. birds, mammals, reptiles) are imperilled or have gone extinct. In 1989, Williams *et al*. (1989) reported that approximately 360 freshwater fish species in North America warranted protection because of their rarity. By 2008, 700 taxa (species, subspecies and distinct populations) were classified as vulnerable, threatened, or endangered (Jelks *et al*. 2008). Because of the poor conservation status of freshwater fishes, research is needed to determine the factors influencing fish assemblages. Although a number of habitat variables (e.g. depth, substrate composition, flow) have been shown to influence the occurrence of fishes in lotic ecosystems (e.g. Moerke & Lamberti 2003; Goldstein & Meador 2005; Toft *et al*. 2007), these relationships are largely based on studies in small streams (Schlosser 1982; Angermeier & Schlosser 1987; Fischer & Paukert 2009). Only recently has research focused on the relationship between fish assemblages and habitat in large rivers (Yoder & Smith 1999; Angradi 2006; Emery *et al*. 2006).

Large rivers are unique and dynamic ecosystems that not only serve commercial and recreational needs but also support high biodiversity of aquatic and semi-aquatic species. Unfortunately, large rivers are also some of the most severely degraded ecosystems in the United States (Rinne *et al*. 2005). The U.S. Environmental Protection Agency (EPA) has declared 45% of the Nation's rivers and streams as 'impaired' (United States Environmental Protection Agency 2002). Because large rivers are a product of smaller streams and rivers in a watershed, large rivers are highly

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susceptible to pollution and other forms of habitat degradation (Flotemersch *et al.* 2006). Degradation of river systems has resulted in a consequent decline of fishes (Jelks *et al.* 2008).

Large rivers are categorised as those that are 'non-wadeable' and those classified as 'great rivers' (Flotemersch *et al.* 2006). Non-wadeable rivers are typically 5th through 7th order rivers that often have extensive areas too shallow to be navigated with a propeller-driven motor and are interspersed with deeper holes that cannot be safely waded (Flotemersch *et al.* 2001). Great rivers (e.g. Mississippi, Missouri and Ohio rivers) are also too deep to wade; they are typically 8th order or greater (Vannote *et al.* 1980; Ward & Stanford 1995). Great rivers were historically well-connected with their floodplains and often have established backwater areas and other lentic habitats. In the midwestern USA, most research has focused on great rivers (Yoder & Smith 1999; Angradi 2006; Emery *et al.* 2006), and data from other non-wadeable rivers are limited (Lyons *et al.* 2001).

Iowa has more than 115 000 km of streams and rivers within its borders [Iowa Department of Natural Resources (IDNR) 2007], of which approximately 5500 km are non-wadeable (i.e. 5th order and larger, excluding the Mississippi and Missouri rivers). In Iowa, agriculture is considered the single greatest factor influencing rivers, and subsequently fish assemblages (Zohrer 2006). More than 80% of Iowa's landscape has been altered by agriculture (Natural Resources Conservation Service 2000). Menzel *et al.* (1984) found that fish assemblages were highly influenced by the effects of agriculture on Iowa streams (i.e. high nutrient loads, fine-particulate substrates, extensive channelisation, little instream vegetation). The degraded condition of many of Iowa's waterways has caused a subsequent decline in fish populations. Approximately 68 (44%) of the 144 native fish species in Iowa are identified as species of greatest conservation need (SGCN) by the IDNR (Zohrer 2006). Sixty-one of these SGCN can be found in non-wadeable rivers (Pflieger 1997). Because of the difficulties associated with sampling fishes in non-wadeable systems (i.e. shallow water, abundant woody debris, deep holes) and a historic focus on sport fishes (Paragamian & Wiley 1987; Paragamian 1989), little is known about the ecology, distribution and abundance of native fishes in Iowa's non-wadeable rivers. A better understanding of fish assemblages (e.g. distribution, abundance of species, habitat and species associations) is critical for the proper management and conservation of Iowa's aquatic resources. As such, the purpose of this research was to describe and evaluate factors influencing fish assemblages in Iowa's non-wadeable rivers.

Methods

Sampling design and reach selection

A non-wadeable river is defined here as any river where fish sampling cannot be conducted safely or effectively using sampling methods typically used in wadeable streams (i.e. backpack- or barge-mounted electric fishing equipment; Flotemersch *et al.* 2006). Many rivers in Iowa are non-wadeable during spring floods; however, these same systems may be relatively shallow (<0.25 m deep) during the summer. Thus, a non-wadeable river is defined as one that has enough deep water to make sampling with backpack or barge-mounted electric fishing unsafe during most of the year. In Iowa, these systems are generally 5th order and greater (Gallagher 1999).

Sampling reaches were selected to ensure that a diversity of different river systems was sampled based on drainage basin, watershed size, stream width and level of disturbance. Access points were then randomly selected from those available. The length of a sampling reach varied depending on the stream order. Sampling reaches in 5th order rivers were 3 km long and reaches in 6th and 7th order rivers were 5 km long. The starting point where a reach began was selected at random. Beginning at the upper terminus of each reach, the reach was divided into 100-m long sections resulting in 30 sections on 5th order rivers and 50 sections on 6th and 7th order rivers. Reaches were never within 1.5 km of a dam or the entry of another non-wadeable river.

Fish sampling

After identifying the 100-m sections, half of the sections were randomly selected (i.e. 15 sections in 5th order rivers, 25 sections in 6th and 7th order rivers) to be sampled using a modified Missouri trawl and a bag seine; the other sections were sampled with boat-mounted electric fishing equipment. All fish sampling occurred during the summer after high spring flows had receded.

Trawling has been used to sample fish assemblages in both lentic and lotic habitats (Kjelson & Johnson 1978; Stockwell *et al.* 2007). The modified Missouri trawl (hereafter, trawl) is a benthic trawl that is particularly useful for sampling small-bodied fishes in large river systems (Herzog *et al.* 2005). The trawl opening was 2.4 m wide and 0.6 m high. The trawl was constructed with an inner trawl body of larger mesh (34.9-mm bar mesh) and outer cover of smaller mesh (6.3-mm Delta, knotless mesh). The result was a large-mesh trawl body inside a small-mesh trawl body that prevented smaller specimens from being damaged by larger specimens or debris. Towlines on the trawl were 21.7 m long that allowed for a 7:1 drop ratio at our expected maximum depth of about 3.1 m. Doors 52 cm long × 32 cm high were used to keep the trawl open. Attached to the footrope was 1.8 m of 4.7 mm chain that ensured the footrope was in constant contact with the river bottom. Further detail on the design and development of this style of trawl can be found in Herzog *et al*. (2005).

Trawls were pulled from the bow as the boat backed downstream as described in Herzog *et al*. (2005). Three trawls were hauled in each section. Each individual trawl continued until it became snagged or until 50 m had been fully trawled. The first haul sampled the thalweg area and the other two hauls sampled non-thalweg areas with random starting points. Fish were processed after each individual haul and the sampling distance was recorded.

Sections sampled with the trawl were also sampled with a bag seine. The seine was 3.6 m long and 1.2 m deep, with 6.3-mm Delta, knotless mesh. A round bag (0.9 m diameter × 0.9 m deep) was centred both vertically and horizontally in the seine. Three, 10-m seine hauls were completed per section. The seine was pulled in a downstream direction parallel to the shore in areas not sampled with the trawl. Fish were processed from each individual seine haul.

Sections not sampled with the trawl and seine were sampled with a boat-mounted, VVP-15B electric fisher (Smith-Root Inc., Vancouver, WA, USA) powered by a 5000-W generator. Electric output was 40 Hz pulsed DC, and power output was standardised to 3000 W based on water conductivity and anode exposure (Burkhardt & Gutreuter 1995). Electric fishing consisted of a single pass with two netters. Electric fishing proceeded in a downstream direction and sampled thalweg and channel border habitat (e.g. banks, woody debris, logs, holes) in each section. Fish were netted using dipnets with 6.3-mm Delta, knotless mesh.

The first 400 individuals of each species collected by each gear in each reach were measured to the nearest millimetre. Total length was measured for all fish except fork length was measured for shovelnose sturgeon, *Scaphirhynchus platorynchus* (Rafinesque). All remaining individuals were counted. All individuals were examined for deformities, eroded fins, lesions and tumours (DELTs), fin clips and tags. Five voucher specimens, as well as any unidentified species, were euthanised using tricaine methanesulfonate (MS-222), preserved in 10% formalin and transported to the laboratory for identification. Protected species were not preserved. Species that were too large to be easily preserved were photographed.

Habitat sampling

The habitat assessment protocol was developed by consulting the IDNR wadeable streams physical habitat assessment (Wilton 2004) and the EPA non-wadeable river protocol (Flotemersch *et al*. 2001). The IDNR wadeable streams protocol was developed for smaller streams and is based on the EPA's wadeable streams physical habitat methods. The EPA's non-wadeable protocol is based on protocols developed for the EPA Environmental Monitoring and Assessment Program (EMAP), EPA Rapid Bioassessment Protocol, U.S. Geological Survey National Water Quality Assessment Program and Maryland DNR–Maryland Biological Stream Survey (Flotemersch *et al*. 2001).

Habitat was measured at the boundary between fish sampling sections, hereafter referred to as a transect. Wetted channel width and bank-full width (i.e. normal high water mark) were measured to the nearest 0.5 m using a laser range finder. Water depth was measured at seven, evenly spaced sampling locations across each transect using a sounding pole or sounding rope if the depth was greater than the length of the 3-m pole. Depth was recorded to the nearest decimetre. As a result of sampling logistics, depth measurements were taken on different dates than fish sampling. To account for differences in stage, depth measurements were corrected to the date of fish sampling based on U.S. Geological Survey gauge readings. Secchi depth and water temperature were measured at the transect point closest to the thalweg every 3 h during sampling. Water velocity was measured using a Marsh McBirney Flo-Mate Portable Velocity Meter (Model 2000; Marsh-McBirney Inc., Frederick, MD, USA) mounted on the sounding pole. Current velocity was measured ~2 cm off the bottom and at 60% of the depth when depth was < 1 m (modified from Kaufmann *et al*. 1999; Flotemersch *et al*. 2001); velocity was measured at 20 and 80% of the depth when depth exceeded 1 m. Depending on depth, substrate was sampled at each of the seven equally spaced points along the transect using the bottom of the sounding pole or by hand (Platts *et al*. 1983). Substrate was classified using a modified Wentworth scale as coarse particulate organic matter, clay (< 0.004 mm), silt (0.004–0.062 mm), sand (0.062–2 mm), gravel (2–64 mm), cobble (64–256 mm), boulder (> 256 mm), or bedrock (Orth & Maughan 1982).

Woody debris, boulders, and other structure located in a 2-m band centred on the transect (i.e. 1 m upstream and 1 m downstream of the transect line) were measured (modified from Kaufmann *et al.* 1999). Surface area and volume of different cover types were estimated from measurements of length, width and depth of individual cover. Woody debris was classified as tree fall, submerged tree, root-wad, log pile-single, log pile-multiple, debris dam or stump. A tree fall was a tree that had fallen into the river, but the root mass remained on the bank. A submerged tree was a fallen tree that was fully submerged. A debris dam differed from a log pile-multiple in that it blocked off more than 50% of the main channel or mouth of a side channel or tributary. Only woody debris > 0.2 m diameter and 0.5 m long was measured. Out-of-water structure that would be submerged at bank-full water level was also recorded using the same categories.

Bank classification, substrate, vegetation and angle were recorded for the left and right bank. The bank assessments were based on the area 1 m upstream and 1 m downstream of the habitat transect line and extending 2 m vertically from the water level (modified from Kaufmann *et al.* 1999). Bank classifications were sandbar, sloping bank, undercut bank, eroding cut-bank and other. Bank substrate was estimated as the percentage of silt, sand, gravel, cobble, boulder, bedrock, clay pan, vegetated soil and other. The percentage of bank vegetation cover (roots, grass, forbs, shrubs, trees, bare ground and other) was also recorded. Angle(s) for the bank were recorded for the 2-m vertical section by measuring the rise and run of each unique bank angle up to 2 m above the waterline.

Floodplain characteristics were recorded at each transect for both sides of the bank. Beginning at the bank (0 m) and ending at 500 m, the dominant land use, cover type and tree species (if present) were recorded (modified from Flotemersch *et al.* 2006). Canopy cover was measured using a convex densiometer as an aerial percentage of overhanging canopy (Murphy *et al.* 1981).

Habitat characteristics were grouped and summarised for data analysis. Total instream cover was the sum of all instream cover including woody debris and boulders. Total out-of-stream cover was the sum of all cover measured on the bank including vegetation, roots, woody debris and boulders. Substrates were grouped into fine and large; fine substrate was the sum of silt and sand substrates, and large substrate was the sum of cobble and boulder. The remaining substrate types (coarse particulate organic matter, clay and bedrock) each accounted for < 1% of the total substrate sampled and were not included in the analysis. Additionally, the coefficient of variation in stream flow was selected as a potential habitat variable because it served as both a measure of flow and also of available habitat (i.e. cover, refuge from high flow) or habitat heterogeneity. Finally, the proportion of depths > 2 m was selected as a measure of the amount of deepwater habitat.

Data analysis

The fish assemblage was quantified in several ways. Species richness and the Shannon-Weaver diversity index (H'; Krebs 1999) were calculated for each reach. Catch data were combined across sampling gears and catch rate (C/f) was calculated as the number of fish per 100 m. Although separate analyses by gear were considered, each reach received the same sampling effort from the same gears allowing that data to be pooled.

Fish assemblage structure was first evaluated using a cluster analysis following Cairns and Kaesler (1971). A Jaccard similarity matrix was created using the presence-absence data of all 84 species. This matrix was then clustered using the unweighted pair-group method with arithmetic mean (UPGMA) and a dendrogram was constructed. The cluster analysis was completed using NTSYSpc (Rohlf 2005).

Relationships between fish assemblages and habitat characteristics were further evaluated using non-metric multidimensional scaling (NMDS; Ruetz *et al.* 2007) to ordinate the sample reaches based on similarity of the fish assemblages. Reaches with similar assemblages are located close together and reaches with dissimilar assemblages are farther apart on NMDS axes (Kruskal & Wish 1984). Non-metric multidimensional scaling is well suited to ecological and community data as it is unconstrained by environmental variables (McCune & Grace 2002). Environmental variables can then be fit to the ordination as vectors to identify environmental gradients. Two NMDS analyses were constructed, one using presence-absence data and the other using species C/f. Both ordinations were completed using the Bray-Curtis distance measure in PC-ORD (McCune & Mefford 1999). Rare species were not removed from the analyses because the majority of species sampled were categorised as rare. In addition, rare species may be particularly sensitive to habitat alterations, and their occurrence is important in detecting habitat characteristics and environmental change (Cao *et al.* 1998).

Habitat variables were summarised using descriptive statistics (minimum, maximum and mean) and correlated with NMDS axes scores. Habitat variables that had an r-value >0.30 were retained and fit to the NMDS ordinations as vectors. Vectors indicated the direction and strength of the correlation between the ordination and the habitat variable (McCune & Grace 2002).

Reaches were grouped based on results of the cluster analysis and ordinations. Multi-response permutation procedures (MRPP) were performed on the ordinations to test the hypothesis of no difference between groups (McCune & Grace 2002). The MRPP yields an A-statistic that represents a chance-corrected within-group agreement value. When all species are identical within groups, A equals one. If heterogeneity within groups equals that which is possible by chance alone, then A equals zero. Negative A-values indicate that there is less heterogeneity within groups than expected by chance. The MRPP also tests whether groups are significantly different. The Sorensen distance measure was used in the MRPP analysis. A Bonferroni correction was used to correct for multiple pair-wise comparisons when more than two groups were present. An indicator species analysis (ISA) was also performed to determine which species had the greatest influence on the groupings (Dufrene & Legendre 1997; McCune & Grace 2002; Toft *et al.* 2007). Finally, chi-square tests were performed to supplement the ISA and to determine whether the occurrence of each species differed among groups. A chi-square test was performed among all groups, and then individual tests were performed between pairs of groups. A Bonferroni correction was used to account for multiple comparisons. The MRPP and ISA analyses were performed using PC-ORD (McCune & Mefford 1999).

Multivariate analysis of variance (MANOVA) was used to determine whether habitat variables identified as important in the NMDS-habitat correlations (i.e. $r > 0.30$) differed among groups identified by ordination. Proportion data were arcsine-square-root transformed (Zar 1984). If MANOVA results were significant, then one-way ANOVA was used to determine how variables differed among groups. Chi-square tests, MANOVA and ANOVA were performed in SAS version 9.1 (SAS Institute 2005) using $\alpha = 0.05$.

Results

Fish assemblages

Ten, 3-km reaches and 11, 5-km reaches were sampled on 16 different rivers in the summers of 2007 and 2008 (Fig. 1). A total of 21 292 individual fish were collected representing 17 families and 84 species (Table 1).

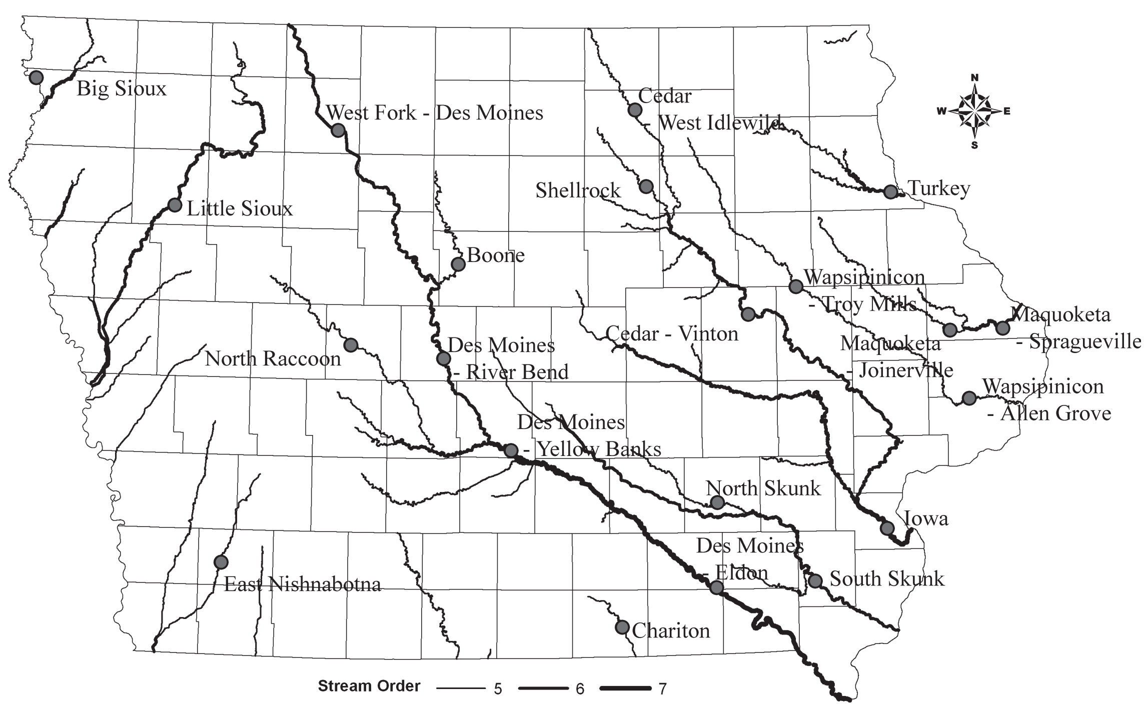

Figure 1. Location of 21 reaches sampled in Iowa non-wadeable rivers, 2007–2008. Stream order is indicated by line thickness.

Table 1. Fishes sampled from 21 reaches in Iowa non-wadeable rivers, 2007–2008

Family and species	Scientific name	SGCN	Catch rate	Total	Frequency
Acipenseridae					
Shovelnose sturgeon	*Scaphirhynchus platorynchus* (Rafinesque)	Y	0.018 ± 0.116	40	24
Lepisosteidae					
Spotted gar	*Lepisosteus oculatus* Winchell	Y	0.001 ± 0.007	2	10
Longnose gar	*Lepisosteus osseus* (Linnaeus)	Y	0.028 ± 0.138	43	19
Shortnose gar	*Lepisosteus platostomus* Rafinesque		0.041 ± 0.155	57	38
Hiodontidae					
Goldeye	*Hiodon alosoides* (Rafinesque)	Y	0.015 ± 0.095	23	29
Mooneye	*Hiodon tergisus* Lesueur		0.010 ± 0.069	15	14
Clupeidae					
Skipjack herring	*Alosa chrysochloris* (Rafinesque)	Y	0.001 ± 0.005	1	5
Gizzard shad	*Dorosoma cepedianum* (Lesueur)		0.374 ± 2.059	1,110	48
Cyprinidae					
Central stoneroller	*Campostoma anomalum* (Rafinesque)		0.001 ± 0.009	12	14
Grass carp	*Ctenopharyngodon idella* (Valenciennes)		0.001 ± 0.011	2	5
Red shiner	*Cyprinella lutrensis* (Baird & Girard)		0.003 ± 0.017	627	33
Spotfin shiner	*Cyprinella spiloptera* (Cope)		*	2,509	86
Common carp	*Cyprinus carpio* Linnaeus		0.299 ± 0.599	404	100
Gravel chub	*Erimystax x-punctatus* (Hubbs & Crowe)	Y	0.009 ± 0.045	314	10
Western silvery minnow	*Hybognathus argyritis* Girard	Y	0.059 ± 0.184	2	10
Brassy minnow	*Hybognathus hankinsoni* Hubbs		*	8	10
Mississippi silvery minnow	*Hybognathus nuchalis* Agassiz	Y	*	86	10
Plains minnow	*Hybognathus placitus* Girard	Y	0.315 ± 1.500	9	5
Bighead carp	*Hypophthalmichthys nobilis* (Richardson)		0.001 ± 0.008	1	5
Common shiner	*Luxilus cornutus* (Mitchill)		0.020 ± 0.102	37	19
Shoal chub	*Macrhybopsis aestivalis* (Gilbert)	Y	0.758 ± 2.471	442	57
Silver chub	*Macrhybopsis storeriana* (Kirtland)		0.002 ± 0.008	68	62
Hornyhead chub	*Nocomis biguttatus* (Kirtland)		0.001 ± 0.008	1	5
Emerald shiner	*Notropis atherinoides* Rafinesque		0.136 ± 0.412	391	71
River shiner	*Notropis blennius* (Girard)		0.047 ± 0.344	36	10
Bigmouth shiner	*Notropis dorsalis* (Agassiz)		0.015 ± 0.065	240	33
Ozark minnow	*Notropis nubilus* (Forbes)	Y	0.005 ± 0.042	1	5
Rosyface shiner	*Notropis rubellus* (Agassiz)		0.172 ± 0.390	57	24
Sand shiner	*Notropis stramineus* (Cope)		0.007 ± 0.035	4,208	95
Mimic shiner	*Notropis volucellus* (Cope)		0.004 ± 0.016	309	19
Channel shiner	*Notropis wickliffi* Trautman		0.004 ± 0.014	171	24
Suckermouth minnow	*Phenacobius mirabilis* (Girard)		*	8	19
Bluntnose minnow	*Pimephales notatus* (Rafinesque)		0.044 ± 0.126	613	67
Fathead minnow	*Pimephales promelas* Rafinesque		0.028 ± 0.109	83	71
Bullhead minnow	*Pimephales vigilax* (Baird & Girard)		0.012 ± 0.040	171	48
Longnose dace	*Rhinichthys cataractae* (Valenciennes)	Y	0.108 ± 0.556	3	10
Blacknose dace	*Rhinichthys obtusus* Agassiz		*	6	5
Creek chub	*Semotilus atromaculatus* (Mitchill)		0.025 ± 0.169	44	33
Catostomidae					
River carpsucker	*Carpiodes carpio* (Rafinesque)		0.011 ± 0.084	503	86
Quillback carpsucker	*Carpiodes cyprinus* (Lesueur)		0.347 ± 1.086	299	100
Hybrid carpsucker	*Carpiodes* spp.		0.073 ± 0.356	95	33
Highfin carpsucker	*Carpiodes velifer* (Rafinesque)		0.051 ± 0.301	110	43
White sucker	*Catostomus commersonii* (Lacepède)		0.002 ± 0.012	25	38
Blue sucker	*Cycleptus elongatus* (Lesueur)	Y	0.700 ± 2.255	5	14
Northern hog sucker	*Hypentelium nigricans* (Lesueur)		0.262 ± 0.795	174	52
Smallmouth buffalo	*Ictiobus bubalus* (Rafinesque)		0.013 ± 0.048	75	57
Bigmouth buffalo	*Ictiobus cyprinellus* (Valenciennes)		0.003 ± 0.017	67	57
Silver redhorse	*Moxostoma anisurum* (Rafinesque)		0.560 ± 1.300	6	14
River redhorse	*Moxostoma carinatum* (Cope)	Y	0.004 ± 0.020	17	5
Golden redhorse	*Moxostoma erythrurum* (Rafinesque)		0.099 ± 0.337	794	67
Shorthead redhorse	*Moxostoma macrolepidotum* (Lesueur)		0.060 ± 0.179	752	100

Table 1. (Continued)

Family and species	Scientific name	SGCN	Catch rate	Total	Frequency
Ictaluridae					
Yellow bullhead	*Ameiurus natalis* (Lesueur)		0.108 ± 0.556	7	10
Channel catfish	*Ictalurus punctatus* (Rafinesque)		0.056 ± 0.166	2,871	95
Black bullhead	*Ictiobus niger* (Rafinesque)		0.205 ± 0.386	5	14
Stonecat	*Noturus flavus* Rafinesque		0.006 ± 0.050	482	57
Flathead catfish	*Pylodictis olivaris* (Rafinesque)		0.003 ± 0.020	85	62
Esocidae					
Northern pike	*Esox lucius* Linnaeus		0.007 ± 0.030	9	19
Umbridae					
Central mudminnow	*Umbra limi* (Kirtland)	Y	0.001 ± 0.008	1	5
Salmonidae					
Rainbow trout	*Oncorhynchus mykiss* (Walbaum)		0.001 ± 0.008	1	5
Percopsidae					
Trout-perch	*Percopsis omiscomaycus* (Walbaum)	Y	*	1	5
Fundulidae					
Blackstripe topminnow	*Fundulus notatus* (Rafinesque)	Y	*	1	5
Moronidae					
White bass	*Morone chrysops* (Rafinesque)		0.071 ± 0.296	160	33
Centrarchidae					
Northern rock bass	*Ambloplites rupestris* (Rafinesque)		0.017 ± 0.110	18	24
Green sunfish	*Lepomis cyanellus* Rafinesque		0.021 ± 0.077	28	48
Pumpkinseed	*Lepomis gibbosus* (Linnaeus)		0.001 ± 0.010	2	5
Orangespotted sunfish	*Lepomis humilis* (Girard)		0.010 ± 0.033	64	48
Bluegill	*Lepomis macrochirus* Rafinesque		0.074 ± 0.180	117	67
Smallmouth bass	*Micropterus dolomieu* Lacepède		0.167 ± 0.511	215	67
Largemouth bass	*Micropterus salmoides* (Lacepède)		0.005 ± 0.027	12	29
White crappie	*Pomoxis annularis* Rafinesque		0.006 ± 0.028	11	24
Black crappie	*Pomoxis nigromaculatus* (Lesueur)		0.014 ± 0.047	20	38
Gasterosteidae					
Brook stickleback	*Culaea inconstans* (Kirtland)		*	3	5
Percidae					
Western sand darter	*Ammocrypta clara* Jordan & Meek	Y	*	22	14
Rainbow darter	*Etheostoma caeruleum* Storer		*	5	10
Iowa darter	*Etheostoma exile* (Girard)		*	1	5
Johnny darter	*Etheostoma nigrum* Rafinesque		0.001 ± 0.002	33	33
Banded darter	*Etheostoma zonale* (Cope)	Y	0.010 ± 0.052	1,348	29
Logperch	*Percina caprodes* (Rafinesque)	Y	*	1	5
Blackside darter	*Percina maculata* (Girard)	Y	0.003 ± 0.012	100	19
Slenderhead darter	*Percina phoxocephala* (Nelson)	Y	0.003 ± 0.011	227	62
River darter	*Percina shumardi* (Girard)	Y	*	30	19
Sauger	*Sander canadensis* (Griffith & Smith)		0.017 ± 0.075	27	19
Walleye	*Sander vitreus* (Mitchill)		0.044 ± 0.11	73	67
Sciaenidae					
Freshwater drum	*Aplodinotus grunniens* Rafinesque		0.103 ± 0.322	236	57

Species are listed in phylogenetic order by family and then alphabetically by scientific name. Also listed is whether a species is a species of greatest conservation need (SGCN), the mean catch rate (mean number of individuals 100 m^{-1} ± standard deviation), the total number of individuals and the frequency of occurrence (percentage of reaches).
* < 0.001 fish 100 m^{-1}.

Twenty-three SGCN were collected, including one state-threatened species (western sand darter; scientific names are provided in Table 1). Three noteworthy collections were made: the first spotted gar recorded from an interior Iowa's river, the first skipjack herring recorded beyond the lower extremes (i.e. the first few river bends) of Iowa's interior rivers since the early 1900s, and the first western sand darter recorded from an interior Iowa river since 1958.

Sand shiner was the most abundant species followed by channel catfish, spotfin shiner, banded darter and gizzard shad (Table 1). The 63 less abundant species

(75% of all species collected) each comprised <1% of the total catch. Although shorthead redhorse, common carp and quillback carpsucker were not abundant, they were collected in all reaches (Table 1). Four non-native species were sampled: bighead carp, common carp, grass carp and rainbow trout.

Catch rate by reach varied from 5.9 to 44.0 fish per 100 m (mean ± standard deviation; 16.8 ± 11.4). The Maquoketa River at Spragueville had the lowest number of sampled individuals (257), and the greatest number of individuals was sampled from the Shellrock River (2262). This result is especially interesting given that the Maquoketa River at Spragueville was a 5-km reach, while the Shellrock River was a 3-km reach. The Little Sioux River had the lowest species richness (16), whereas the Cedar River at Vinton had the highest species richness (41). Shannon-Weaver diversity index values varied from 1.39 to 2.98 among reaches.

Habitat characteristics

Mean wetted channel width varied from 23.4 to 229.5 m and mean bank-full width varied from 32.7 to 262.9 m among reaches (Table 2). Mean depth varied from 0.5 to 2.3 m. Mean depth on the date of fish sampling varied from 0.7 to 2.8 m. The deepest depth measurement was 18.0 m. Mean current velocity varied from 0.16 to 0.85 m s^{-1}. Reaches were dominated by sand substrate (70 ± 20%), with silt (9 ± 9%), gravel (10 ± 9%) and cobble (9 ± 14%) accounting for relatively equal proportions of the substrate composition. Boulder substrate was rare (2 ± 4%); and coarse particulate organic matter, bedrock and clay were each <1% of the mean substrate.

Measured total instream cover varied from 23 to 779 m^3 (Table 2). Extrapolating the volume of

Table 2. Description and summary statistics of habitat variables measured from 21 reaches in Iowa non-wadeable rivers, 2007–2008

Variable	Description	Mean	SD	Minimum	Maximum
Channel morphology and flow					
Depth	Mean depth (m), corrected to date of fish sampling	1.44	0.54	0.71	2.80
Angle	Mean bank angle (°)	53.25	11.56	30.93	76.89
WCW	Mean wetted channel width (m)	76.54	55.41	23.39	229.47
BFW	Mean bank-full width (m)	92.18	57.32	32.77	262.87
Flow	Mean current velocity (m s^{-1})	0.40	0.19	0.16	0.85
Substrate					
Clay	Mean proportion clay substrate (%)	0.10	0.28	0.00	1.15
Silt	Mean proportion silt substrate (%)	8.35	9.04	0.00	32.86
Sand	Mean proportion sand substrate (%)	70.44	19.76	17.79	96.22
Gravel	Mean proportion gravel substrate (%)	10.31	9.31	0.55	35.13
Cobble	Mean proportion cobble substrate (%)	8.91	14.35	0.00	59.86
Boulder	Mean proportion boulder substrate (%)	1.58	3.92	0.00	16.98
Bedrock	Mean proportion bedrock substrate (%)	0.27	0.95	0.00	4.15
Instream cover					
TF-I	Proportion of total instream cover – tree fall (%)	36.98	31.97	0.00	98.78
ST-I	Proportion of total instream cover – submerged tree (%)	0.77	1.83	0.00	7.70
LP-I	Proportion of total instream cover – log pile (%)	53.12	33.48	0.32	97.68
B-I	Proportion of total instream cover – boulder (%)	3.47	10.13	0.00	38.90
RR-I	Proportion of total instream cover – rip-rap (%)	3.91	9.63	0.00	38.54
Other-I	Proportion of total instream cover – other (%)	1.74	6.19	0.00	28.40
Wood-in	Mean volume of instream woody debris (m^3)	122.17	159.58	17.36	774.10
Rock-in	Mean volume of instream rock (m^3)	7.27	12.59	0.00	41.52
Canopy and bank characteristics					
Canopy	Mean canopy cover (%)	16.86	11.29	3.04	38.75
TF	Proportion of total bank cover – tree fall (%)	12.81	14.68	0.00	42.14
RB	Proportion of total bank cover – roots (%)	12.93	10.38	1.10	34.37
LP	Proportion of total bank cover – log pile & debris dam (%)	19.67	22.51	0.00	79.00
RR	Proportion of total bank cover – rip-rap (%)	11.07	11.25	0.00	43.47
W	Proportion of total bank cover – willow (%)	7.71	16.40	0.00	64.21
NWV	Proportion of total bank cover – non-woody vegetation (%)	35.73	24.92	2.19	93.41
Other	Proportion of total bank cover – other (%)	0.09	0.35	0.00	1.59
Wood-out	Mean volume of bank woody debris (m^3)	108.60	106.62	7.00	479.47
Rock-out	Mean volume of bank rock (m^3)	17.11	17.07	0.00	62.00

instream habitat measured to the size of the sampling reach resulted in a total estimated volume of instream habitat varying from 1174 to 38 958 m^3. Log piles and debris dams accounted for 53% of instream habitat, followed by tree falls (37%), rip-rap (4%), boulders (3%) and standing trees (1%). Other forms of instream cover (e.g. urban refuse) made up about 2% of the total volume of instream cover.

Measured out-of-stream habitat varied from 42 to 629 m^3 (Table 2). The estimated total volume of out-of-stream habitat for an entire sampling reach varied from 2112 to 31 461 m^3. Non-woody vegetation accounted for the greatest percentage of out-of-stream habitat (36%), followed by log piles and debris dams (20%), rootballs and protruding roots (13%), tree falls (12%), rip-rap and boulders (11%), willows (7%) and other (e.g. urban refuse, 1%).

Mean bank angle varied from 30.9° to 76.8° and mean canopy cover varied from 3.0 to 38.8% cover (Table 2). Riparian cover was evaluated as the percentage of each cover type in the area from the river bank to 500 m from the bank and was variable among reaches. Wooded cover type varied from 9 to 97% (mean ± SD: 4 ± 28%,) grass cover type varied from 0 to 18% (2 ± 4%), pasture cover type varied from 0 to 21% (2 ± 6%), row crop cover type varied from 0 to 77% (30 ± 27%) and urban cover type varied from 0 to 10% (1 ± 2%). The cover type that was unknown (i.e. could not be viewed from the river) averaged 11%.

Relationships between fish assemblages and habitat characteristics

Relationships between fish assemblages and habitat characteristics were first evaluated by cluster analysis (Fig. 2). Using the least restrictive pairings of the data, three distinct groups were observed. The first four reaches (i.e. Big Sioux, Chariton, East Nishnabotna and Little Sioux rivers) clustered together and contained the reaches in the Missouri River drainage (hereafter, Missouri River). The last seven reaches (i.e. Boone, Cedar-West Idlewild, Maquoketa-Joinerville, Shellrock, Wapsipinicon-Troy Mills and West Fork Des Moines rivers) also clustered together and were all in the Mississippi River drainage (hereafter, Mississippi River A). Finally, the remaining reaches clustered together, all of which were also in the Mississippi River drainage (hereafter, Mississippi River B).

Relationships between fish assemblages and habitat characteristics were evaluated using NMDS. The first ordination was constructed using presence-absence data (Fig. 3). The resulting ordination was two-

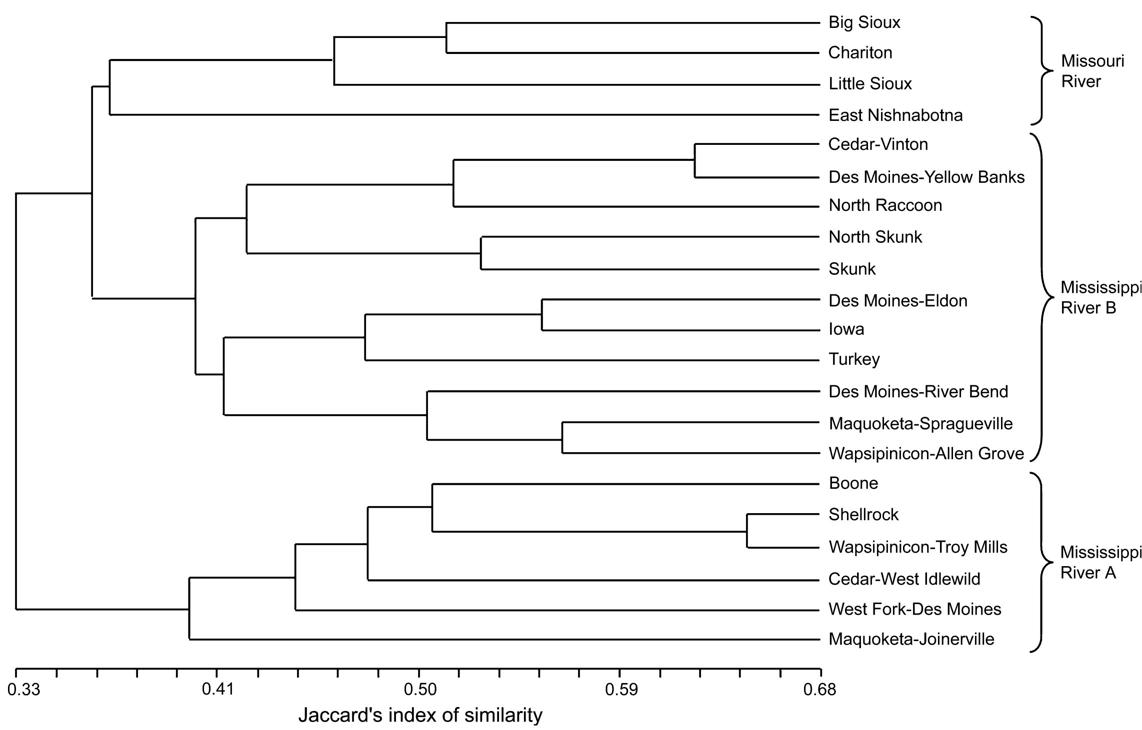

Figure 2. Dendrogram of 21 reaches sampled in Iowa non-wadeable rivers, 2007–2008, based on Jaccard's similarity of fish assemblage using presence-absence data.

dimensional with a final stress of 19.1, a final instability of 0.003 and a *P*-value of 0.004, indicating that obtaining a lower stress with random data was unlikely. Results of the ordination were nearly identical to those from the cluster analysis in that the same three clusters of reaches were easily identified. A MRPP was performed using the three groupings: (1) Missouri River drainage; (2) Mississippi River drainage A; and (3) Mississippi River drainage B. Using the Sorensen distance measure, the resulting chance-corrected within-group agreement (*A*) was 0.15 ($P < 0.001$), indicating significant differences in fish assemblage structure among the groups.

Habitat variables correlated with NMDS scores were the coefficient of variation in stream velocity, corrected mean depth, mean percentage of fine substrate, mean percentage of large substrate, mean wetted channel width and the proportion of depths >2 m (Fig. 3). Selected habitat variables differed among the three groups (Pillai's $\text{trace}_{12,30} = 0.96$, $P = 0.046$); therefore, one-way ANOVAS were conducted. Percent large substrate was not included in the MANOVA because it was highly correlated with percent fine substrate. Individual ANOVAS between groups indicated that only percent fine substrate differed significantly among the three groups ($F_{2,18} = 5.23$, $P = 0.016$); the remaining habitat variable *P*-values varied from 0.05 (mean wetted channel width) to 0.66 (mean depth). Although most habitat variables were not significantly different between groups, several trends were apparent (Fig. 4). Reaches in the Missouri River drainage were typically narrow (mean ± SD: 47 ± 16 m) and had a high proportion of fine substrate (93 ± 3%). Reaches in the Mississippi River A group were also narrow (46 ± 14 m) but typically had a high proportion of large substrate (22 ± 23%) compared with other reaches (4 ± 6%). Reaches in the Mississippi River B group tended to be wider (104 ± 65 m), deeper (1.69 ± 0.58 m) and had a high proportion of fine substrate (83 ± 13%).

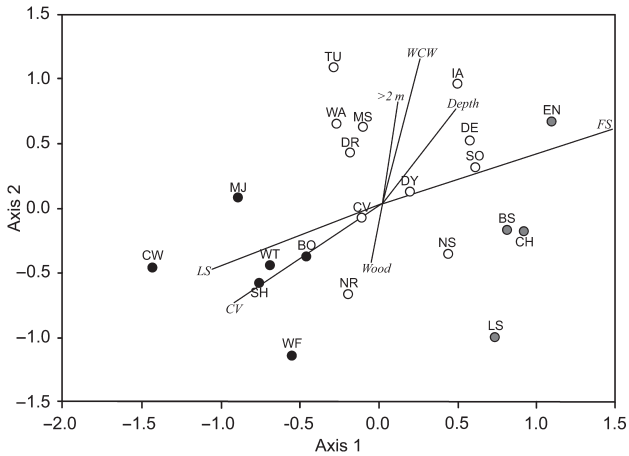

Figure 3. Non-metric multidimensional scaling ordination of fish species presence-absence data from 21 reaches sampled in Iowa non-wadeable rivers, 2007–2008. Grey circles represent reaches in the Missouri River drainage, solid circles represent reaches in the Mississippi River group A and open circles represent reaches in the Mississippi River group B. Sample reach names are abbreviated: Big Sioux (BS), Boone (BO), Chariton (CH), Cedar-Vinton (CV), Cedar-West Idlewild (CW), Des Moines-Eldon (DE), Des Moines-River Bend (DR), Des Moines-Yellow Banks (DY), East Nishnabotna (EN), Iowa (IA), Little Sioux (LS), Maquoketa-Joinerville (MJ), Maquoketa-Spragueville (MS), North Raccoon (NR), North Skunk (NS), Shellrock (SH), Skunk (SO), Turkey (TU), Wapsipinicon-Allen Grove (WA), Wapsipinicon-Troy Mills (WT) and West Fork-Des Moines (WF). Physical habitat variables correlated with the fish assemblage are plotted as vectors indicating the direction of change and strength of correlation. Physical habitat variables are mean wetted channel width (WCW), mean depth (depth), proportion fine substrate (FS), mean volume of instream woody cover (wood), coefficient of variation in stream flow (CV), proportion of large substrate (LS) and proportion of depths >2 m.

The ISA indicated that 14 species were strong indicators of the three groups (Table 3). The strongest indicators in each of the three groups were red shiner and goldeye in the Missouri River group, golden redhorse and slenderhead darter in the Mississippi River A group and flathead catfish and smallmouth buffalo in the Mississippi River B group. The three-way chi-square test indicated only two species (red shiner and white sucker) were strong indicators, but chi-square tests between any two of the groups indicated between two and six strong indicators (Table 4). The most common indicator species were white sucker (three of the four chi-square tests) and red shiner (two of the four chi-square tests). No single indicator species was able to indicate a single group, but the presence of golden redhorse or slenderhead darter indicated that the reach was not in the Missouri River drainage. Additionally, the presence of goldeye, red shiner, smallmouth buffalo or shortnose gar indicated that the reach was not in the Mississippi River A group; and the presence of blackside darter or white sucker indicated that the reach was not in Mississippi River B group.

A second ordination was created using catch rate (Fig. 5). The resulting ordination was three-dimensional with a final stress of 8.4, a final instability of 0.000001, and a *P*-value of 0.004, indicating that obtaining a lower stress with random data was unlikely. The MRPP was performed using the three groupings as before. Using the Sorensen distance measure, the resulting chance-corrected within-group agreement (*A*) equaled 0.054 ($P = 0.017$), suggesting

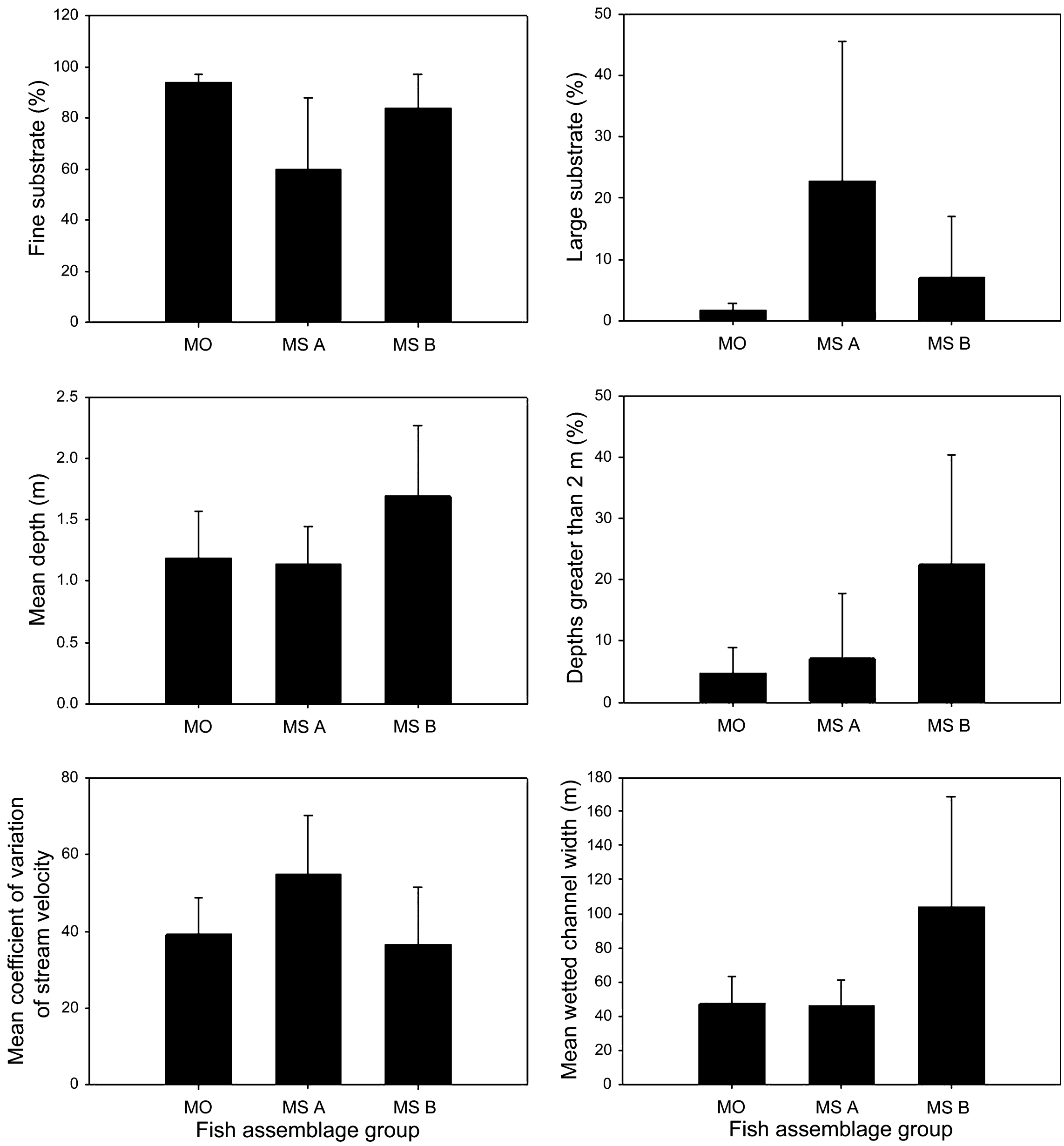

Figure 4. Physical habitat variables from 21 reaches sampled in Iowa non-wadeable rivers, 2007–2008, by fish assemblage group. Groups include the Missouri River drainage (MO) $n = 4$, the Mississippi River group A (MS A) $n = 6$ and the Mississippi River group B (MS B) $n = 11$. Error bars indicate one standard deviation.

significant differences among the groups. However, the resulting MRPP was not significant when Bonferroni corrected for the three groups. Because the groups were not significantly different, indicator species analyses were not performed. Overlaying the selected habitat variables as vectors on the ordinations revealed that six habitat variables had r values > 0.30 in relation to the fish abundance data: the coefficient of variation of stream flow, mean bank angle, mean wetted channel width, percentage large substrate (cobble or boulder), the proportion of depths > 2 m and total instream rocky habitat.

Discussion

Iowa's non-wadeable rivers exhibit high fish species diversity as evidenced by the 84 fish species, or 54% of the fish species known to occur in Iowa, sampled in

Table 3. Statistically significant indicator species from an indicator species analysis for groups of reaches sampled from 21 reaches in Iowa non-wadeable rivers, 2007–2008

Group	Species	IV	*P*
MO	Red shiner	78.6	0.0020
MO	Goldeye	55	0.0182
MO	Silver chub	52.8	0.0226
MO	Shortnose gar	46.7	0.0460
MS A	Golden redhorse	57.9	0.0014
MS A	Slenderhead darter	61.1	0.0022
MS A	Spotfin shiner	44.4	0.0028
MS A	White sucker	66.7	0.0068
MS A	Highfin carpsucker	58	0.0304
MS A	Banded darter	52.4	0.0432
MS A	Creek chub	47.3	0.0450
MS A	Bigmouth shiner	47.3	0.0482
MS B	Flathead catfish	70.6	0.0002
MS B	Smallmouth buffalo	58.7	0.0094

Groups include the Missouri River drainage (MO), the Mississippi River group A (MS A), and the Mississippi River group B (MS B). Also listed is the indicator value (IV) and the corresponding *P*-value for each species.

Table 4. Statistically significant indicator species from chi-square tests for groups of reaches sampled from 21 reaches in Iowa non-wadeable rivers, 2007–2008

MO vs MS A vs MS B	MO vs MS A	MO vs MS B	MS A vs MS B
Red shiner	Gizzard shad	Blackside darter	Smallmouth buffalo
White sucker	Golden redhorse	White sucker	White sucker
	Goldeye		
	Red shiner		
	Shortnose gar		
	Slenderhead darter		

Groups include the Missouri River drainage (MO), the Mississippi River group A (MS A), and the Mississippi River group B (MS B).

this study. Fish assemblages could be categorised as belonging to one of three major groups. The three groups of reaches and associated fish assemblages were likely related to stream geomorphology (i.e. depth, stream gradient, substrate, width). Stream theory suggests that stream gradient decreases, and depth, channel width and the proportion of fine substrate increases as a river flows downstream (Vannote *et al.* 1980). Reaches in the Mississippi River A group were characteristic of 'headwater' or lower order streams because they had a high proportion of large substrate and relatively shallow, narrow channels. By contrast, reaches in the Mississippi River B group had higher proportions of fine substrate, were deeper and were relatively wide. Smith and Hubert (1989) examined habitat and fish assemblages in the Powder River of Wyoming. The mainstem of the Powder River was similar to reaches in the Mississippi River B group with fine substrate and wide channels. Tributaries to the Powder River had geomorphic characteristics (e.g. depth, substrate, width) similar to Mississippi River A reaches. Many of the warmwater species in the Powder River were the same as those most common in Mississippi River B reaches (e.g. shovelnose sturgeon, sauger), and many of the species in the Powder River tributaries were the same species that were grouped in the Mississippi River A group (e.g. fathead minnow, white sucker). These results support the notion of defining groups based on geomorphology, as species in two distinct regions (i.e. Iowa and Wyoming) were affiliated with specific geomorphic characteristics.

Fish assemblages characteristic of the Missouri River drainage included red shiner, shoal chub and western silvery minnow. These three species tend to be more abundant in the Missouri River drainage than in the Mississippi River drainage (Pflieger 1997). Species commonly sampled in Mississippi River A reaches included gravel chub, logperch, rock bass and suckermouth minnow. Species sampled from the Mississippi River A were typically benthic species with strong associations with large substrate (i.e. cobble and boulder; Pflieger 1997). For example, Jones and Maughan (1987) found logperch prefer streams with gravel and rocky bottoms in Oklahoma, and Tiemann *et al.* (2004) found suckermouth minnow in Kansas was most common in reaches characterised by large substrate. In contrast to group A, the fish assemblage in the Mississippi River B group was characterised by species such as gizzard shad, mooneye, shovelnose sturgeon and skipjack herring. Species sampled from the Mississippi River drainage B were typically large river species that prefer fine, shifting substrates (Becker 1983; Pflieger 1997). For instance, Paragamian (1990) found that mooneye and gizzard shad were most commonly sampled over expanses of fine substrate. Similarly, Coker (1930) and Cross and Huggins (1975) found skipjack herring prefer fine substrates.

Reaches in Iowa's non-wadeable rivers with larger substrate were dominated by benthic species (e.g. banded darter, gravel chub, rainbow darter, suckermouth minnow; Pflieger 1997). Rocky habitat and large substrate provide important spawning habitat and create interstitial spaces for invertebrate production (Probst *et al.* 1984; Waters 1995). Large rocks also create eddies that provide refuge from stream flow and accumulate organic matter, both of which are beneficial to fish. Heitke *et al.* (2006) found a positive relationship between boulder abundance and index of

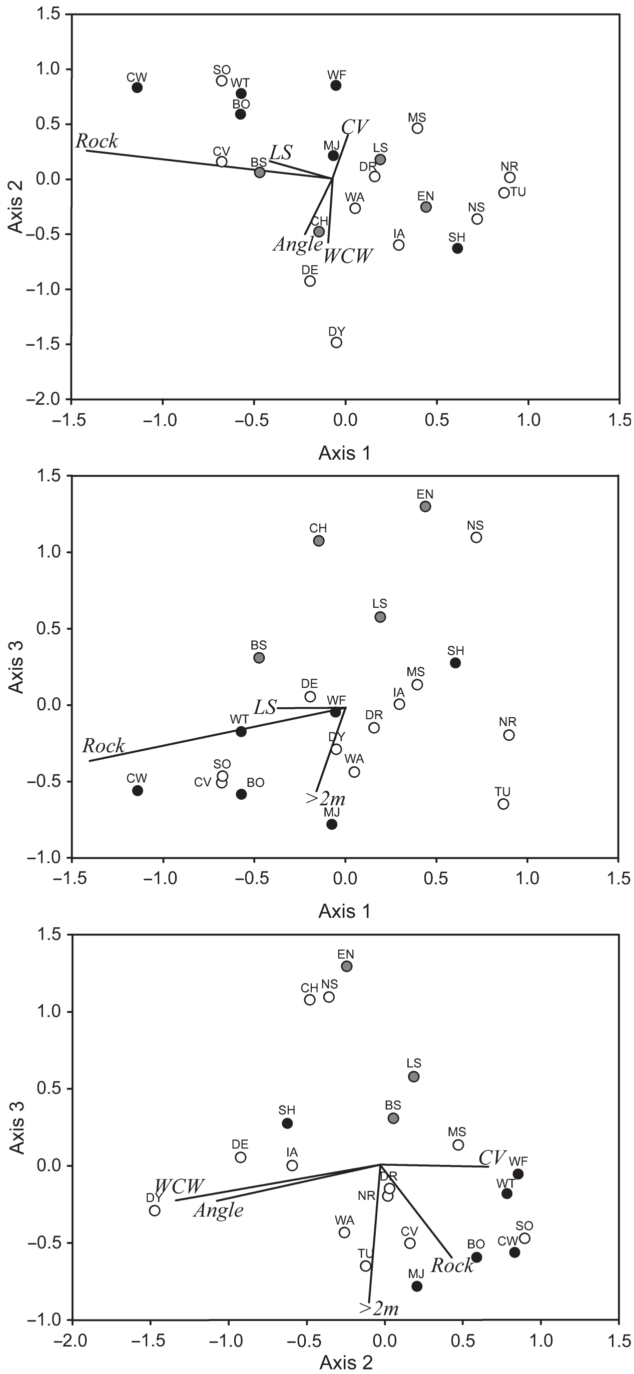

Figure 5. Non-metric multidimensional scaling ordination of fish species abundance data from 21 reaches sampled in Iowa non-wadeable rivers, 2007–2008. Physical habitat variables correlated with the fish assemblage are plotted as vectors indicating the direction of change. Grey circles represent reaches in the Missouri River drainage, solid circles represent reaches in the Mississippi River group A and open circles represent reaches in the Mississippi River group B. Sample reach names are abbreviated: Big Sioux (BS), Boone (BO), Chariton (CH), Cedar-Vinton (CV), Cedar-West Idlewild (CW), Des Moines-Eldon (DE), Des Moines-River Bend (DR), Des Moines-Yellow Banks (DY), East Nishnabotna (EN), Iowa (IA), Little Sioux (LS), Maquoketa-Joinerville (MJ), Maquoketa-Spragueville (MS), North Raccoon (NR), North Skunk (NS), Shellrock (SH), Skunk (SO), Turkey (TU), Wapsipinicon-Allen Grove (WA), Wapsipinicon-Troy Mills (WT) and West Fork-Des Moines (WF). Physical habitat variables are mean wetted channel width (WCW), mean depth (depth), proportion fine substrate (FS), mean volume of instream woody cover (wood), coefficient of variation in stream flow (CV), proportion of large substrate (LS), proportion of depths > 2 m, mean volume of instream rocky cover (rock) and mean bank angle (angle).

biotic integrity scores in Iowa streams. Lobb and Orth (1991) found that total fish abundance in large warmwater streams was greatest in riffle habitats dominated by large substrates. Additionally, boulders were the second strongest indicator of fish assemblage composition in streams draining agricultural lands in the upper Midwest (Talmage *et al.* 2002). Reaches associated with large substrate were also associated with greater coefficients of variation of stream flow. Coefficient of variation in stream flow was selected as a potential habitat variable because it served not only as a measure of flow, but also of available habitat (i.e. cover, refuge from high flow) or habitat heterogeneity. Many studies have found that the availability of cover is directly related to species richness (Pusey *et al.* 1993). Additionally, Angermeier and Schlosser (1989), and Johnson and Jennings (1998) found that the number of fish species increased as habitat heterogeneity increased. Traditionally, species richness was thought to be most closely related to area (Williams 1964), where the number of species sampled increases as the area sampled increases. Williams (1964) also proposed the idea that species richness may be related to habitat diversity, and recent studies (e.g. Baldi 2007) suggest that habitat heterogeneity may have a larger role in estimating species richness than species–area relationships.

Reaches with a high proportion of fine substrate also tended to have a high proportion of depths >2 m and wide channels. In general, these were higher order reaches located closer to the river's terminus at either the Mississippi or Missouri rivers. These reaches were dominated by small-bodied fishes not associated with benthic habitats (e.g. mimic shiner, channel shiner) or large river benthic species (e.g. blue sucker, shovelnose sturgeon). A number of studies have shown that large river benthic species are associated with expanses of fine substrate. For example, Curtis *et al.* (1997) and Quist *et al.* (1999) found shovelnose sturgeon were most common over sand substrate in large rivers. Additionally, a number of cyprinid species (e.g. *Macrhybopsis* spp., *Notropis* spp.) prefer open-channel areas with fine substrates (Harlan *et al.* 1987; Eberle *et al.* 1997; Pflieger 1997).

Although several species had clear associations with habitat, the majority of species sampled in this study were not strongly associated with specific habitat characteristics. A number of factors may explain this pattern. One explanation is that many fishes in Iowa's non-wadeable rivers are naturally tolerant species. Fish assemblages in prairie streams and rivers have adapted to the dynamic and often extreme environmental conditions (Matthews 1988; Dodds *et al.* 2004), resulting in fish assemblages dominated by habitat, trophic and reproductive generalists (Fausch & Bestgen 1997; Bramblett *et al.* 2005). An alternative explanation is that aquatic habitat in Iowa has been degraded by the effects of urbanisation and agriculture (Menzel *et al.* 1984). Historically, Iowa's non-wadeable rivers may have supported a diversity of fishes that varied among rivers, but as a result of degradation of habitat and loss of intolerant species, these rivers are now more homogeneous and dominated by generalist species (Heitke *et al.* 2006; Palic *et al.* 2007). Examples of habitat generalists in this study included the three species sampled in all reaches (common carp, quillback carpsucker, shorthead redhorse), as well as channel catfish, green sunfish and sand shiner. Lobb and Orth (1991), Kinsolving and Bain (1993) and Guenther and Spacie (2006) also found many of these species to be habitat generalists in their study systems.

Non-wadeable rivers are diverse ecosystems that serve a variety of needs and must, therefore, be managed carefully. Historic management practices have focused primarily on sport fish species (Paragamian & Wiley 1987; Paragamian 1989), however, only 14 of the 84 species sampled in this study can be described as sport fish (Harlan *et al.* 1987). The remaining 70 species are important components of aquatic food webs and are critical for ecosystem function (Bertrand & Gido 2007; Herwig & Zimmer 2007). More research is needed in similar systems to define or quantify the differences between groups identified by fish assemblage and habitat variables and to better understand the ecology of fishes in non-wadeable systems.

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