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Abstract

Fish assemblages in rivers of the Midwestern United States are an important component of the region's natural resources and biodiversity. We characterized the physical environment and presence of dams in a series of reaches in three eastern Iowa rivers tributary to the Mississippi River and related these characteristics to the fish assemblages present. Some physical characteristics were similar among the 12 study reaches, whereas others differed substantially. We found a total of 68 species across the 12 study reaches; 56 in the Turkey River, 51 in the Maquoketa River and 50 in the Wapsipinicon River. Seventeen species could be described as 'downstream-distributed'; 15 being found only in the lowest reach of one or more rivers and the other two being found only in the lowest reaches or two or more contiguous reaches including the lowest reach. Two species could be described as 'upstream-distributed', being found only in an uppermost reach. Non-metric multidimensional scaling ordination illustrated similarities among reaches, and five physical variables were significantly correlated with assemblage similarities. Catchment area and number of dams between reaches and the Mississippi River were strongly correlated with assemblage similarities, but the directions of their effects were opposite. Catchment area and number of dams were confounded. The collective evidence to date suggests that the pervasiveness of dams on rivers significantly alters fish assemblages, making underlying patterns of species change and relationships with naturally varying and human-influenced physical characteristics along a river's course difficult to discern.

Keywords

depth, fish passage, fragmentation, pools, stream, thalweg

Disciplines

Aquaculture and Fisheries | Environmental Indicators and Impact Assessment | Natural Resources Management and Policy | Terrestrial and Aquatic Ecology

Comments

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FISH ASSEMBLAGE RELATIONSHIPS WITH PHYSICAL CHARACTERISTICS AND PRESENCE OF DAMS IN THREE EASTERN IOWA RIVERS

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ABSTRACT

Fish assemblages in rivers of the Midwestern United States are an important component of the region's natural resources and biodiversity. We characterized the physical environment and presence of dams in a series of reaches in three eastern Iowa rivers tributary to the Mississippi River and related these characteristics to the fish assemblages present. Some physical characteristics were similar among the 12 study reaches, whereas others differed substantially. We found a total of 68 species across the 12 study reaches; 56 in the Turkey River, 51 in the Maquoketa River and 50 in the Wapsipinicon River. Seventeen species could be described as 'downstream-distributed'; 15 being found only in the lowest reach of one or more rivers and the other two being found only in the lowest reaches or two or more contiguous reaches including the lowest reach. Two species could be described as 'upstream-distributed', being found only in an uppermost reach. Non-metric multidimensional scaling ordination illustrated similarities among reaches, and five physical variables were significantly correlated with assemblage similarities. Catchment area and number of dams between reaches and the Mississippi River were strongly correlated with assemblage similarities, but the directions of their effects were opposite. Catchment area and number of dams were confounded. The collective evidence to date suggests that the pervasiveness of dams on rivers significantly alters fish assemblages, making underlying patterns of species change and relationships with naturally varying and human-influenced physical characteristics along a river's course difficult to discern. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS: depth; fish passage; fragmentation; pools; stream; thalweg

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INTRODUCTION

Fish assemblages in rivers of the Midwestern United States are an important and highly visible component of the region's natural resources and biodiversity (Dauwalter *et al.*, 2010; Paukert and Galat, 2010). Fish assemblages play important roles in river ecosystem function (Vanni, 2010) and are a cornerstone of environmental assessment of river health (Simon, 1999). Fish assemblages in agriculturally dominated areas such as the Midwest reflect a combination of natural and anthropogenic influences (Infante and Allan, 2010; NFHB, 2010), and understanding relationships among and relative impacts of the many influences will be necessary to successfully manage and enhance Midwestern rivers and their fish faunas (Kwak and Freeman, 2010).

Sedimentation is one of the most deleterious consequences of agricultural land use for streams and rivers in the Midwestern United States and other agricultural areas

(Waters, 1995; Allan, 2004). Sedimentation has many negative effects on rivers, including reduced light availability, reduced primary productivity, burial of coarse substrates and other types of coverand filling of pools. Filling of pools with sediment has been shown to reduce maximum depths and depth variation, changing the physical character of rivers to the detriment of fish and other riverine biota (Wood and Armitage, 1997; Walser and Bart, 1999; Shields *et al.*, 2007). Agricultural land use is pervasive in Iowa (Whitney, 1994; NRCS, 2009) and has resulted in highly degraded stream habitats and biota (Wilton, 2004; Heitke *et al.*, 2006; Rowe *et al.*, 2009b).

Adequate depth and depth variation associated with the presence of deep pools are important habitat features in rivers for conserving native species and supporting healthy fish assemblages (Rabeni and Jacobson, 2006). Deep pools in Midwestern rivers have been shown to support greater abundance of certain species than shallower areas (Aadland, 1993), and telemetry studies in Iowa rivers have shown that deep pools are preferred by both walleye (Paragamian, 1989) and channel catfish (Gelwicks, 2007) at certain times

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of the year. As an example of the growing recognition of the importance of depth and flow at a much broader scale, the concept of environmental flows is currently one of the most urgent issues in river management worldwide (Postel and Richter, 2003; Bruno and Siviglia, 2012).

Fragmentation by dams and the resulting blockage of upstream–downstream movements can also have significant impacts on river fish assemblages (Dynesius and Nilsson, 1994; Pringle *et al.*, 2000; Rinne *et al.*, 2005). Numerous studies in Midwestern rivers have documented blockage of fish passage and fish assemblage degradation associated with dams and grade control structures (Santucci *et al.*, 2005; IDNR, 2010; Butler and Wahl, 2011; Thomas *et al.*, 2011; Wang *et al.*, 2011). The abundance of dams nationally (Graf, 1999) and the large literature documenting negative effects on fish passage and fish assemblages (Rinne *et al.*, 2005) suggest that these impacts are widespread. The large number of dams and other man-made structures impeding fish passage in Iowa rivers and streams (IDNR, 2010; IWC, 2011; Thomas *et al.*, 2011) suggest that these impacts are probably also common in Iowa.

The importance of deep pools to many riverine fish species, the documented preference of some species for deep pools in Iowa rivers and the pervasive agricultural land use that reduces availability of deep pools in Iowa rivers led us to hypothesize that spatial differences in fish assemblage structure might be related to the availability of deep pool habitat. We also hypothesized that dams could play a role, fragmenting portions of rivers and limiting access in all but the lowermost reaches to the deep pool habitat and diverse species pool downstream in the Mississippi River. The overall goal of our study was to characterize the physical environment and presence of dams in a series of reaches in three eastern Iowa rivers and relate these characteristics to the fish assemblages present. Special emphasis was placed on examining relationships with depth characteristics. Specific objectives were to (i) quantify thalweg depth and pool characteristics continuously throughout reaches; (ii) quantify other physical characteristics and presence of downstream dams at the reach scale; (iii) characterize fish assemblages at the reach scale by compiling recent sampling records within reaches; and (iv) explore relationships of fish assemblages with physical characteristics and presence of downstream dams.

STUDY AREA

Our study focused on three rivers in northeastern Iowa, the Maquoketa, Turkey and Wapsipicon (Figure 1). Study reaches were determined on the basis of interest from state management biologists and availability of boat access. The Maquoketa River is 240 km long and occupies a catchment

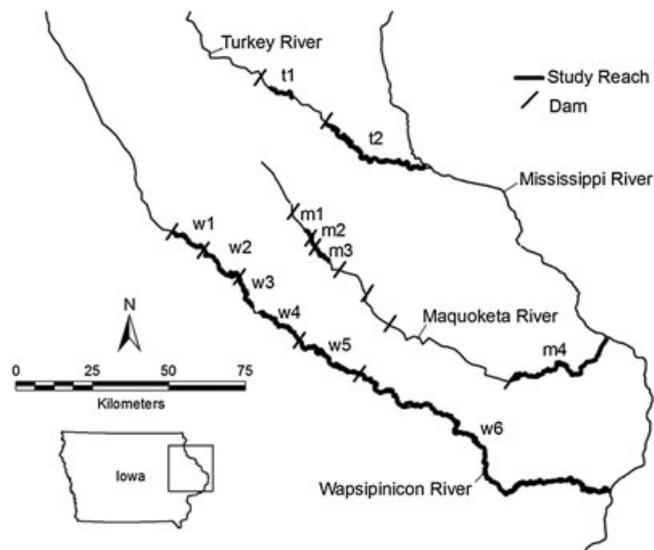


Figure 1. Locations of 12 study reaches examined for relationships of fish assemblages with physical, thalweg depth and pool characteristics in three eastern Iowa rivers

of 4387 km² (USGS, 2011). Four reaches in the Maquoketa River (Table I) were sampled, all fifth order at their upstream ends, but the furthest downstream reach is sixth order at its downstream end. The Turkey River is similar in size, 246 km long and occupies a catchment of 4384 km². Two reaches in the Turkey River (Table I) were sampled, both fifth order at their upstream ends, but the furthest downstream reach is sixth order at its downstream end. The Wapsipicon River is the longest of the three rivers at 480 km and occupies the largest catchment at 6565 km². Six reaches in the Wapsipicon River (Table I) were sampled, all fifth order at both their upstream and downstream ends. All three rivers flow in a southeasterly direction and are tributary to the Mississippi River, the Maquoketa entering the upper portion of Pool 13 below Bellevue, Iowa, the Turkey entering the upper portion of Pool 11 below Guttenberg, Iowa, and the Wapsipicon entering the middle portion of Pool 14 below Clinton, Iowa (Figure 1). Each of the three rivers has several dams (Figure 1; Table I) of various heights and other design characteristics (IDNR, 2004a; IDNR, 2010; IWC, 2011). One of the dams on the Maquoketa River, the Delhi Dam, made national news in July 2010 when it was washed out after heavy rains.

The three rivers flow through three of Iowa's 10 ecoregions (Griffith *et al.*, 1994). Both Turkey River reaches are in the Paleozoic Plateau (PP) ecoregion, which differs from all other Iowa ecoregions due to its lack of recent glaciations, greater topographic relief, abundant limestone outcrops and aquifers and relatively thinner soils. Wadeable streams in the PP tend to be cooler and shadier, have greater

Table I. Physical characteristics of 12 study reaches in three eastern Iowa rivers. Catchment area was calculated from the upstream end of the reach. Downstream dams is defined as the number of dams between the reach and the Mississippi River. Reach locations are shown in Figure 1

Reach	River	Catchment Area (km ²)	Sinuosity	Slope (%)	Downstream Dams
M1	Maquoketa	419.7	1.53	0.0231	6
M2	Maquoketa	427.7	1.42	0.0340	5
M3	Maquoketa	704.1	2.59	0.0583	4
M4	Maquoketa	4249.8	1.53	0.0623	0
T1	Turkey	2109.5	1.56	0.0388	1
T2	Turkey	2708.3	1.86	0.0561	0
W1	Wapsipinicon	2306.3	1.38	0.0311	4
W2	Wapsipinicon	2804.0	1.61	0.0368	3
W3	Wapsipinicon	2983.4	1.48	0.0348	2
W4	Wapsipinicon	3132.7	1.49	0.0306	2
W5	Wapsipinicon	3257.7	1.69	0.0403	1
W6	Wapsipinicon	4026.1	1.65	0.0391	0

width-to-depth ratios, steeper slopes, coarser substrates and healthier and more diverse fish assemblages than streams in other ecoregions (Wilton, 2004; Heitke *et al.*, 2006; Rowe *et al.*, 2009a). The lowest reaches in the Maquoketa and Wapsipinicon Rivers are in the Southern Iowa Rolling Loess Prairies (RLP) ecoregion, characterized by moderately rolling topography and loess soils of moderate depth. Wadeable streams in the RLP tend to have gentler slopes than the PP and have substrates dominated by sand and silt. All reaches upstream of the lowest reach in the Maquoketa and Wapsipinicon Rivers are in the Iowan Surface (IS) ecoregion, which is a zone of transition between the PP and the flatter topography, loamier soils, extensive artificial drainage and intensive row crop agriculture of the Des Moines Lobe ecoregion to the west. Wadeable streams in the IS have ratios of fine to coarse substrates intermediate between the other two ecoregions, and although slopes are generally comparable with the RLP, temperatures are cooler in many IS streams due to contributions from limestone aquifers as in the PP.

METHODS

Physical characteristics and presence of dams

We obtained physical characteristics of study reaches, including catchment area, sinuosity, channel slope and locations of dams from existing databases. Catchment area, sinuosity and channel slope were obtained from the Iowa Stream Reach Dataset (Loan-Wilsey *et al.*, 2005). Locations of dams were obtained from the State of Iowa Inventory of Dams (IDNR, 2004a). Dam locations were used to calculate the number of downstream dams, defined as the number of dams on the river between the downstream end of the reach and the Mississippi River. This characteristic was used as an

index of fragmentation, representing the number of barriers to passage between reaches and larger, deeper and more species-rich waters of the Mississippi River downstream.

We determined thalweg depth and pool characteristics of study reaches by continuous thalweg depth surveys during June–September, 2003–2004. Surveys were carried out from a boat using a Global Positioning System (GPS)-equipped Marinetek PCS200 echosounder, which recorded depth and position three times per second onto a laptop computer. Surveys began at the uppermost point of a study reach and proceeded downstream slowly, following the thalweg and recording depths and positions along the entire reach. Surveys were conducted at or near average flow conditions, and daily stage records from the USGS gauging station in or nearest to each reach were used to standardize measured depths by differences between mean daily stages recorded on the day of surveys and the mean stages for that month and day over the entire period of record.

Because of various small errors in GPS positioning, raw spatial positions of depths typically deviated slightly from the thalweg when superimposed on digital orthophotos. To establish a line of depth points approximating the thalweg, we drew a line down the middle of the river channel on digital orthophotos (IDNR, 2004b) and raw depth positions were superimposed on this line by moving the shortest distance to the line. Because of differences in boat speed and adjusting positions of depth points to a mid-channel line, the length intervals between raw depth points on this line were unequal. To adjust the distance between depth points, a series of 1 m intervals was superimposed on the line of raw depth points, and the closest raw depth to the endpoint of each 1 m interval was used to create a new series of depth points. The resulting series of depths, standardized to average stage and adjusted to consistent 1 m intervals along the thalweg of each study reach, was used in

subsequent analyses of thalweg depth and pool characteristics. GIS manipulations were performed in ArcView GIS 3.2 (ESRI, 2006).

We calculated nine variables expressing thalweg depth and pool characteristics for each study reach from the series of standardized and adjusted thalweg depths. Thalweg depth variables included mean depth, median depth and depth coefficient of variation. Pools were defined as continuous portions of reaches with thalweg depth ≥ 2 m. Variables describing pool characteristics included pool percentage of reach, pool density (number of pools per kilometer), mean pool length, pool length coefficient of variation, mean inter-pool distance (average distance between pools) and inter-pool distance coefficient of variation.

Fish assemblages

We characterized fish assemblages in study reaches using data from multiple sources, including samples collected as part of other studies (Wilton, 2004; Loan-Wilsey *et al.*, 2005; Gelwicks, 2007) as well as samples collected for this study. Because the purpose was to characterize and compare fish assemblages with physical characteristics at the reach scale, all known samples that targeted the entire fish assemblage were considered for inclusion. To limit potential biases due to different sampling methodologies and efficiencies in different conditions, presence/absence data were used. To limit potential influence of historical trends in species occurrence (Sindt *et al.*, 2011, 2012), only samples from 1990 to 2006 were included. Samples were collected from June to October.

We collected fish by single-pass, daytime, pulsed-direct current (DC) electrofishing and depending on reach width and depth at the time of sampling either a barge or boat electrofisher was used. Length of river sampled varied depending on wetted width and was approximately equal to 40 times the mean wetted width. Most samples were collected by boat electrofishing with three workers, proceeding slowly downstream and moving back and forth across the thalweg in an attempt to cover all major macrohabitats and cover objects. When reaches were too shallow to boat effectively, a barge electrofisher operated by three or more workers proceeded upstream with dipnetters moving back and forth across the channel in an attempt to cover all major macrohabitats and cover objects. Collected fish were placed in tubs with fresh water, identified to species, tallied, and returned alive to the river. Samples collected as part of other studies (Wilton, 2004; Loan-Wilsey *et al.*, 2005; Gelwicks, 2007) used similar methods.

Data analysis

We examined differences among study reaches based on thalweg depth and pool characteristics by comparing graphs

of individual variables and collectively using non-metric multidimensional scaling (NMDS) ordination. For ordinations, thalweg depth and pool variables were first normalized (mean = 0, standard deviation = 1), then a 12×12 Euclidean Distance matrix was calculated, and finally the matrix was used as input to the NMDS ordination. The normalization, distance matrix and NMDS ordination were generated using PRIMER (Clarke and Gorley, 2006).

We also examined similarities in the fish assemblages present among study reaches and relationships with physical characteristics and presence of dams using NMDS ordination. The fish collections described earlier were used to compile a reach-by-species presence-absence matrix, then a 12×12 Bray-Curtis similarity matrix was calculated, and finally the matrix was used as input to the NMDS ordination. No species were omitted from the analysis. Variables expressing physical characteristics and presence of dams that were significantly correlated with ordination axes were shown as vectors indicating direction of most significant gradient, with vector lengths indicating relative strengths of the relationships. The similarity matrix, NMDS ordination and vectors were generated using PRIMER (Clarke and Gorley, 2006). Correlations of NMDS axis scores from the thalweg depth/pool ordination with axis scores from the fish assemblage ordination were examined using the CORR procedure in SAS (SAS Institute, 2009).

We evaluated differences in physical characteristics and presence of dams between study reaches where fish species were present and absent with Wilcoxon Rank Sum exact tests using the NPAR1WAY procedure in SAS (SAS Institute, 2009).

RESULTS

Physical characteristics and presence of dams

Some physical characteristics were similar among the 12 study reaches, whereas others differed substantially (Table I). Sinuosity of 11 of the reaches was similar, ranging only from 1.38 to 1.86, whereas reach M3 on the Maquoketa River had a much higher sinuosity value of 2.59. All 12 reaches were low gradient with similar % slope values ranging from 0.0231% to 0.0623%. Other physical characteristics differed markedly among reaches, due to both natural drainage patterns and human influences. Catchment areas ranged tenfold, from 420 to 4250 km². The number of downstream dams ranged from zero for the lower most reaches in each of the three rivers to six in reach M1 on the Maquoketa River.

Thalweg depth characteristics differed among the 12 reaches but to a lesser extent than some other physical characteristics (Figure 2). Reach M2 on the Maquoketa River, both Turkey River reaches, and reaches W1 and W3-W5

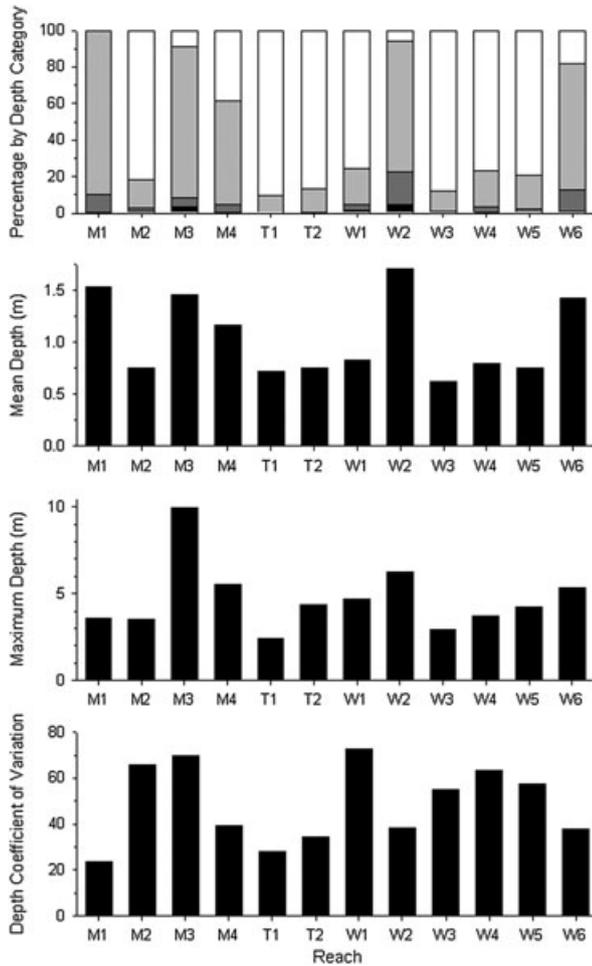


Figure 2. Thalweg depth characteristics of 12 reaches on three eastern Iowa rivers. The top panel shows the percentage of thalweg lengths in each of four depth categories: >3 m (black); 2–3 m (dark gray); 1–2 m (light gray); <1 m (white)

on the Wapsipinicon River were predominantly shallower than 1 m. Reaches M1, M3 and M4 on the Maquoketa and reaches W2 and W6 on the Wapsipinicon were predominantly between 1 and 2 m deep. Thalweg depths greater than 2 m were uncommon, except for reach W2 where they occurred in 22.5% of the reach. Thalweg depths greater than 3 m were rare, ranging from absent in reaches T1 and W3 to a maximum of 4.5% of reach W2. Mean thalweg depths ranged from 0.6 m in reach W3 to 1.7 m in reach W2, both on the Wapsipinicon River. Maximum thalweg depths ranged from 2.4 m in reach T1 to 10 m in reach M3; most of the other study reaches had maximum thalweg depths between 3 and 6 m. The thalweg depth coefficient of variation ranged from 23 in reach M1 to 73 in reach W1.

Pool characteristics differed markedly among the study reaches (Figure 3). The pool percentage of reaches ranged from 0.07% in reach T1 to 22.5% in reach W2. Pool density

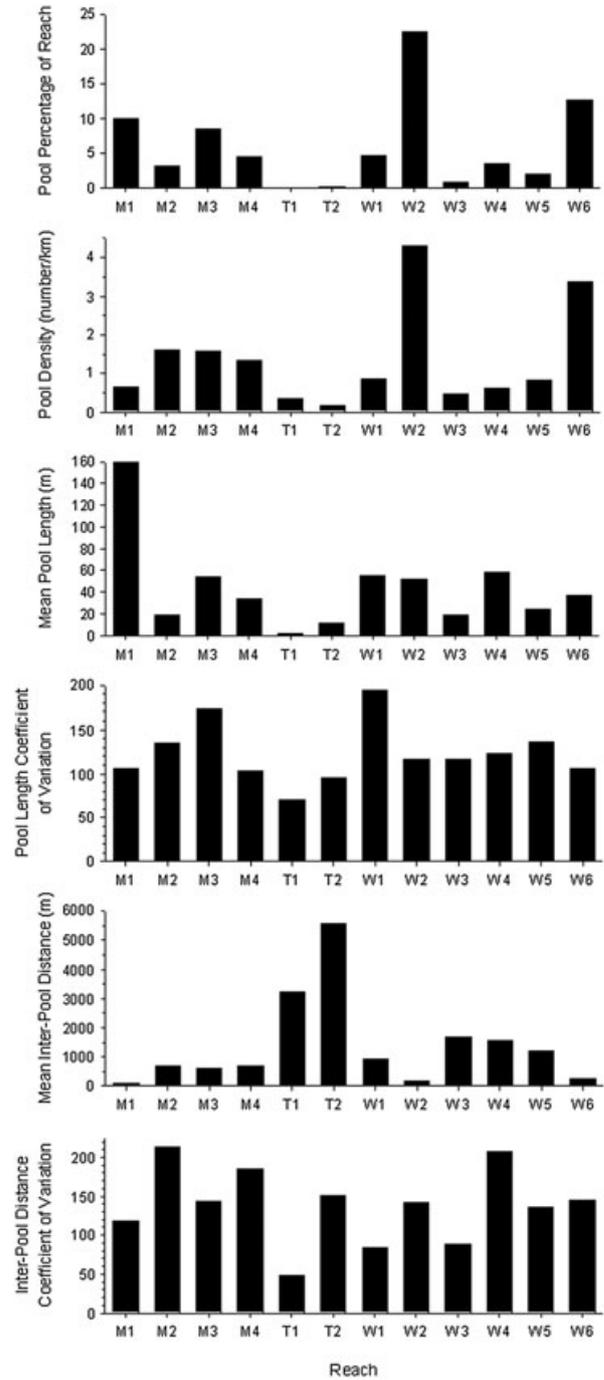


Figure 3. Pool characteristics of 12 reaches on three eastern Iowa rivers. Pools are defined as continuous portions of reaches with thalweg depth ≥ 2 m

ranged from 0.17 pools/km in reach T2 to 4.3 pools/km in reach W2. Mean pool length ranged from 2 m in reach T1 to 159 m in reach M1. Pool length coefficient of variation ranged from 71 in reach T1 to 195 in reach W1. Mean inter-pool distance ranged from 85 m in reach M1 to 5.6 km in

reach T2. Inter-pool distance coefficient of variation ranged from 49 in reach T1 to 213 in reach M2.

Ordination of the study reaches based on the nine variables describing thalweg depth and pool characteristics provided an integrated picture of similarities and differences among reaches (Figure 4). The two-dimensional ordination had a stress value of 0.08, indicating a good depiction of relative similarities among reaches and no chance of misleading interpretation (Clarke and Warwick, 2001). The two Turkey River reaches grouped closely and apart from reaches in the other two rivers, reflecting their uniform shallowness and lack of pools (Figures 2 and 3). Reaches at the other end of the Depth 1 axis, including W2 and W6 on the Wapsipinicon and M1 and M3 on the Maquoketa, tended to be the deepest with the greatest mean depths and pool percentages. Although generally the deepest, these four reaches did not group closely on the ordination, reflecting differences in other characteristics such as the uniquely great maximum depth of M3, large pool percentage of W2 and great mean pool length of M1. The other six reaches grouped fairly close together reflecting similar thalweg depth and pool characteristics, with the minor exception of greater variation in depth and pool length in W1.

Fish assemblages

The samples we obtained revealed a total of 68 species across the 12 study reaches (Table II). Eighteen are considered sensitive species (Wilton, 2004), 14 are species of greatest conservation need (SGCN) (Zohrer, 2005) and one (common carp) is non-native. Six species, including common carp, golden redhorse, northern hog sucker, quillback carpsucker,

smallmouth bass and walleye, were found in all 12 reaches. Thirteen species, including black bullhead, bowfin, burbot, crystal darter, longnose dace, longnose gar, mimic shiner, Mississippi silvery minnow, Mooneye, Ozark minnow, rainbow darter, shoal chub and shortnose gar, were found in only one reach. Seventeen species could be described as 'downstream-distributed'; 15 of those, including freshwater drum, gizzard shad, sauger, shovelnose sturgeon, silver chub, bowfin, burbot, crystal darter, longnose dace, longnose gar, mimic shiner, Mississippi silvery minnow, mooneye, shoal chub and shortnose gar being found only in the lowest reach of one or more rivers and the other two, bigmouth buffalo and smallmouth buffalo, being found only in lowest reaches or two or more contiguous reaches including the lowest reach. Two species, black bullhead and rainbow darter, could be described as 'upstream-distributed', being found only in an uppermost reach.

The Turkey River had the largest number of species, 56, compared with 51 species in the Maquoketa River and 50 in the Wapsipinicon River (Table II). More sensitive species, tolerant species and SGCN were found in the Turkey River than the other two rivers. Numbers of sensitive species were 12, 14 and 10, numbers of tolerant species were 7, 8 and 6 and numbers of SGCN were 6, 10 and 7 in the Maquoketa, Turkey and Wapsipinicon Rivers, respectively.

Ordination of the study reaches based on presence-absence of the 68 fish species provided an integrated picture of fish assemblage similarities and differences among study reaches (Figure 5). The two-dimensional ordination had a stress value of 0.07, indicating a good depiction of relative similarities among reaches and no chance of misleading interpretation (Clarke and Warwick, 2001). The lowest reaches in each of the three rivers were separated widely from the other reaches at the lowest values of the Fish 1 axis. The two uppermost reaches in the Maquoketa River were at the other end of the Fish 1 axis. The two Turkey River reaches were separated widely from the other reaches at the lowest values of the Fish 2 axis, although they were separated widely from each other along the Fish 1 axis.

Five variables expressing physical characteristics and presence of dams were significantly correlated ($p < 0.05$) with ordination axes and were plotted as vectors on the ordination (Figure 5, top). Downstream dams (+) and catchment area (−) had the strongest relationships with the Fish 1 axis, and slope (−) had a similar but weaker relationship with Fish 1. Depth coefficient of variation (+) and mean inter-pool distance (−) had relationships with the Fish 2 axis that were opposing but similar in strength. The strongest underlying relationships were the negative correlation ($r = -0.88$, $p = 0.0002$) of the Fish 1 axis with catchment area and positive correlation ($r = 0.89$, $p = 0.0001$) with the number of downstream dams (Figure 6). The fish assemblages in all three rivers followed a very similar pattern of

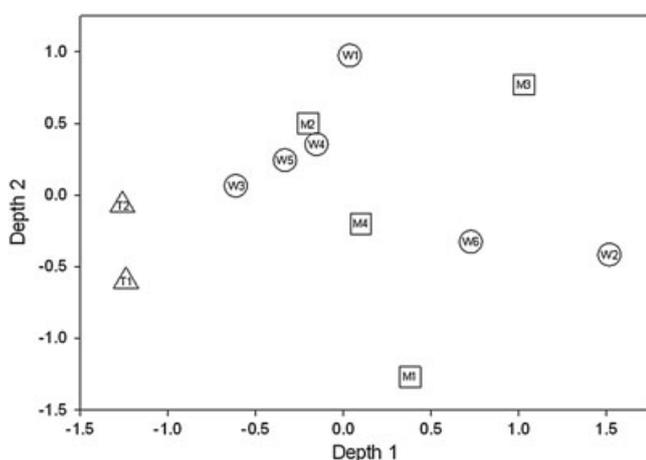


Figure 4. Non-metric multidimensional scaling ordination of 12 reaches in three eastern Iowa rivers based on thalweg depth and pool characteristics. Maquoketa River reaches are represented by squares, Turkey River reaches by triangles, and Wapsipinicon River reaches by circles. Reaches are identified inside symbols

Table II. Fish species collected from 12 reaches in three eastern Iowa rivers. Species are listed in descending order of percent occurrence in all reaches. Tolerance ratings (Wilton, 2004) are: T=tolerant, I=intermediate, S=sensitive. An 'x' in the species of greatest conservation need (SGCN) column indicates species of greatest conservation need (Zohrer 2005). Distribution codes, listed separately for each species in each river, are: A=found in all reaches, L=found in lowest reach only, D=found only in two or more contiguous reaches including the lowest reach, U=found only in uppermost reach or contiguous reaches including uppermost reach, S=found in some reaches, N=not found.

Common name	Scientific name	Tolerance Rating	SGCN	% Reaches Present	Distribution code		
					Maq. R.	Tur. R.	Wap. R.
Common carp ¹	<i>Cyprinus carpio</i>	T		100	A	A	A
Golden redhorse	<i>Moxostoma erythrurum</i>	I		100	A	A	A
Northern hog sucker	<i>Hypentelium nigricans</i>	S		100	A	A	A
Quillback carpsucker	<i>Carpiodes cyprinus</i>	I		100	A	A	A
Smallmouth bass	<i>Micropterus dolomieu</i>	S		100	A	A	A
Walleye	<i>Sander vitreus</i>	I		100	A	A	A
Black crappie	<i>Pomoxis nigromaculatus</i>	I		92	A	L	A
Largemouth bass	<i>Micropterus salmoides</i>	I		92	U	A	A
Spotfin shiner	<i>Cyprinella spiloptera</i>	I		92	A	L	A
Bluegill	<i>Lepomis macrochirus</i>	I		83	U	A	U
Bluntnose minnow	<i>Pimephales notatus</i>	T		83	U	A	U
Highfin carpsucker	<i>Carpiodes velifer</i>	I		83	D	A	A
Northern pike	<i>Esox lucius</i>	S		83	D	U	A
Sand shiner	<i>Notropis stramineus</i>	I		83	U	L	A
Shorthead redhorse	<i>Moxostoma macrolepidotum</i>	I		83	D	A	A
White sucker	<i>Catostomus commersoni</i>	I		83	A	A	S
Channel catfish	<i>Ictalurus punctatus</i>	I		75	D	L	A
Green sunfish	<i>Lepomis cyanellus</i>	T		75	A	U	S
Northern rock bass	<i>Ambloplites rupestris</i>	S		67	S	A	S
Orangespotted sunfish	<i>Lepomis humilis</i>	I		67	U	A	D
Bigmouth buffalo	<i>Ictiobus cyprinellus</i>	I		58	D	N	D
Bullhead minnow	<i>Pimephales vigilax</i>	I		58	L	L	S
Common shiner	<i>Luxilus cornutus</i>	I		58	U	A	U
River carpsucker	<i>Carpiodes carpio</i>	I		58	D	A	S
Silver redhorse	<i>Moxostoma anisurum</i>	I		58	L	L	U
Emerald shiner	<i>Notropis atherinoides</i>	I		50	D	A	D
Johnny darter	<i>Etheostoma nigrum</i>	I		50	S	L	S
Banded darter	<i>Etheostoma zonale</i>	S	x	42	S	A	S
Bigmouth shiner	<i>Notropis dorsalis</i>	T		42	S	L	S
Rosyface shiner	<i>Notropis rubellus</i>	S		42	S	L	U
White crappie	<i>Pomoxis annularis</i>	I		42	N	N	S
Yellow bullhead	<i>Ameiurus natalis</i>	I		42	S	N	S
Brassy minnow	<i>Hybognathus hankinsoni</i>	I		33	U	L	D
Central stoneroller	<i>Campostoma anomalum</i>	I		33	S	A	N
Flathead catfish	<i>Pylodictis olivaris</i>	I		33	L	L	S
Redfin shiner	<i>Lythrurus umbratilis</i>	I	x	33	N	A	D
White bass	<i>Morone chrysops</i>	I		33	D	L	L
Black buffalo	<i>Ictiobus niger</i>	I	x	25	L	N	S
Blackside darter	<i>Percina maculata</i>	S	x	25	S	N	S
Creek chub	<i>Semotilus atromaculatus</i>	T		25	U	A	N
Fathead minnow	<i>Pimephales promelas</i>	T		25	U	L	S
Freshwater drum	<i>Aplodinotus grunniens</i>	I		25	L	L	L
Gizzard shad	<i>Dorosoma cepedianum</i>	T		25	L	L	L
Hornyhead chub	<i>Nocomis biguttatus</i>	S		25	S	N	U
River shiner	<i>Notropis blennioides</i>	I		25	N	A	L
Sauger	<i>Stizostedion canadense</i>	I		25	L	L	L
Shovelnose sturgeon	<i>Scaphirhynchus platyrhynchus</i>	S	x	25	L	L	L
Smallmouth buffalo	<i>Ictiobus bubalus</i>	I		25	L	N	D
Black redhorse	<i>Moxostoma duquesnei</i>	S	x	17	S	L	N
Fantail darter	<i>Etheostoma flabellare</i>	I		17	N	A	N
Silver chub	<i>Macrhybopsis storeriana</i>	I		17	L	L	N
Slenderhead darter	<i>Percina phoxocephala</i>	S	x	17	N	L	S
Stonecat	<i>Noturus flavus</i>	I		17	S	L	N

(Continues)

Table II. (Continued)

Common name	Scientific name	Tolerance Rating	SGCN	% Reaches Present	Distribution code		
					Maq. R.	Tur. R.	Wap. R.
Suckermouth minnow	<i>Phenacobius mirabilis</i>	I		17	N	L	S
Yellow bass	<i>Morone mississippiensis</i>	I		17	S	N	N
Black bullhead	<i>Ameiurus melas</i>	T		8	N	U	N
Bowfin	<i>Amia calva</i>	I	x	8	N	N	L
Burbot	<i>Lota lota</i>	I	x	8	N	L	N
Crystal darter	<i>Crystallaria asprella</i>	S	x	8	N	L	N
Longnose dace	<i>Rhinichthys cataractae</i>	S	x	8	N	L	N
Longnose gar	<i>Lepisosteus osseus</i>	I	x	8	N	L	N
Mimic shiner	<i>Notropis volucellus</i>	I		8	N	L	N
Mississippi silvery minnow	<i>Hybognathus nuchalis</i>	S	x	8	N	L	N
Mooneye	<i>Hiodon tergisus</i>	S		8	N	L	N
Ozark minnow	<i>Notropis nubilus</i>	S	x	8	S	N	N
Rainbow darter	<i>Etheostoma caeruleum</i>	S		8	U	N	N
Shoal chub	<i>Macrhybopsis hyostoma</i>	S		8	N	L	N
Shortnose gar	<i>Lepisosteus platostomus</i>	I		8	N	N	L

¹Non-native species.

SGCN, species of greatest conservation need

change along the gradients of changing catchment area and number of downstream dams. There were no significant correlations ($p > 0.05$) between axis scores from the thalweg depth/pool and fish assemblage ordinations.

Reaches grouped loosely by ecoregion (Figure 5, bottom), indicating fish assemblage similarities among reaches within ecoregions and differences between reaches. The lowest reaches of the Maquoketa and Wapsipinicon Rivers, in the RLP ecoregion, grouped tightly on the ordination indicating very similar fish assemblages. The two Turkey River reaches, in the PP ecoregion, were grouped loosely and separated from all other reaches by the Fish 2 axis. The remaining reaches, in the IS ecoregion, were also grouped somewhat loosely but separated from reaches in the other ecoregions. Within the IS ecoregion reaches grouped by river, with the Wapsipinicon reaches grouped tightly at intermediate values of the Fish 1 axis and the Maquoketa reaches at larger values.

Our Wilcoxon Rank Sum exact tests identified 11 variables expressing physical characteristics and presence of dams that differed significantly ($p < 0.05$) between reaches where at least one fish species was present versus absent (Table III). The presence of 25 species was related to at least one variable. The number of downstream dams differed significantly between reaches where 12 species were present than where they were absent, including two SGCN (redfin shiner and shovelnose sturgeon). Reaches where species were absent had significantly more downstream dams than where they were present for all but one species (hornyhead chub). Catchment area differed similarly for 11 species, including one SGCN (black buffalo), being greater where seven species were present and greater where the other four species were absent.

Of the 25 species whose presence was significantly associated with one or more variables, four (bigmouth buffalo, smallmouth buffalo, freshwater drum and gizzard shad) were among the downstream-distributed species described previously. The presence of four species, including one SGCN (banded darter), was related to sinuosity, with significantly higher sinuosity where the species were present. Channel slope was significantly greater where three species (emerald shiner, river carpsucker and white bass) were present than where they were absent. The presence of two game fish species, channel catfish and white bass, was related to mean depth, with significantly greater depths where the species were present. Depth coefficient of variation was significantly lower where creek chub and orange-spotted sunfish were present. Presence of fantail darter was related to five pool variables, with pools significantly smaller and less prevalent where fantail darter were present.

DISCUSSION

Despite being fifth order over much or all of their lengths, the 12 study reaches varied considerably as characterized by physical characteristics and presence of dams. Catchment areas varied by an order of magnitude and the number of dams between reaches and the Mississippi River ranged from 0 to 6. Although the magnitude of variation was less, thalweg depth variables illustrated a gradient of reaches from ones that were primarily less than 1 m deep to reaches averaging well above 1 m deep with numerous areas greater than 2 m deep. Maximum depths, representing the deepest

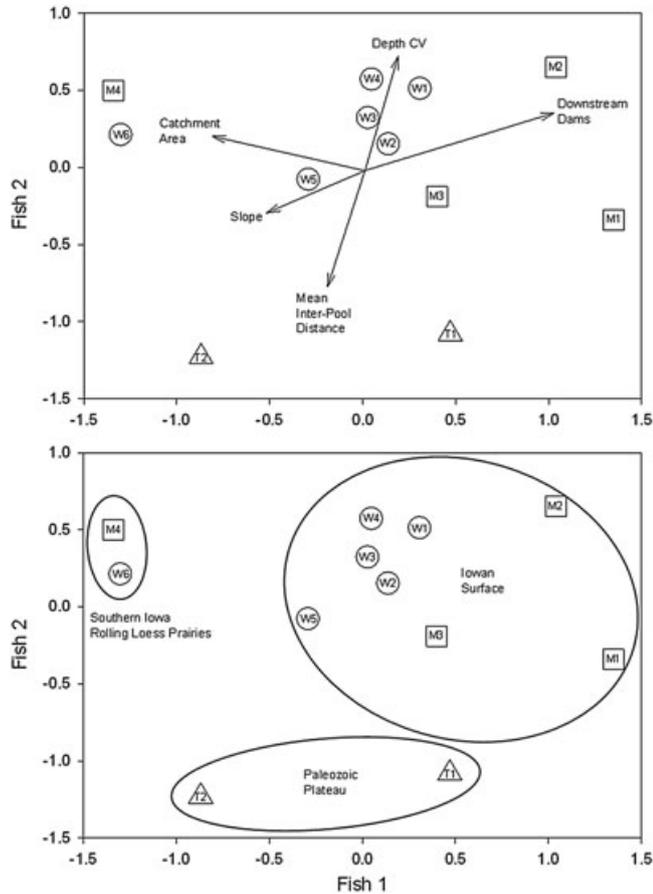


Figure 5. Non-metric multidimensional scaling ordination of 12 reaches in three eastern Iowa rivers based on the presence of fish species. Reaches are identified as in Figure 4. Top panel shows relationships with physical, thalweg depth and pool characteristics as vectors, expressing the joint correlation of the two ordination axes with characteristics. Only characteristics significantly ($p < 0.05$) correlated with one of the ordination axes are shown. Vector lengths indicate relative strength of correlations. Bottom panel shows grouping of reaches by ecoregion

available 'holes' in riverine portions and impoundments upstream of dams, ranged from less than 3 m in two reaches to four reaches greater than 5 m, with one reach having a maximum depth of 10 m. Pools exhibited a much greater magnitude of variation among reaches than thalweg depths themselves. The prevalence, size and distance between pools all varied by over an order of magnitude. Pool density ranged from three reaches with fewer than one pool every 2 km to two reaches with more than 3 pools/km. Mean pool length ranged from 2 m to 159 m. These spectra of variation resulted in widely differing conditions and represent considerable potential influence on fish assemblages inhabiting the 12 study reaches.

Depth has been related to stream fish in numerous studies, as measured in a variety of different ways and at different spatial scales. Deep areas in streams have been shown to

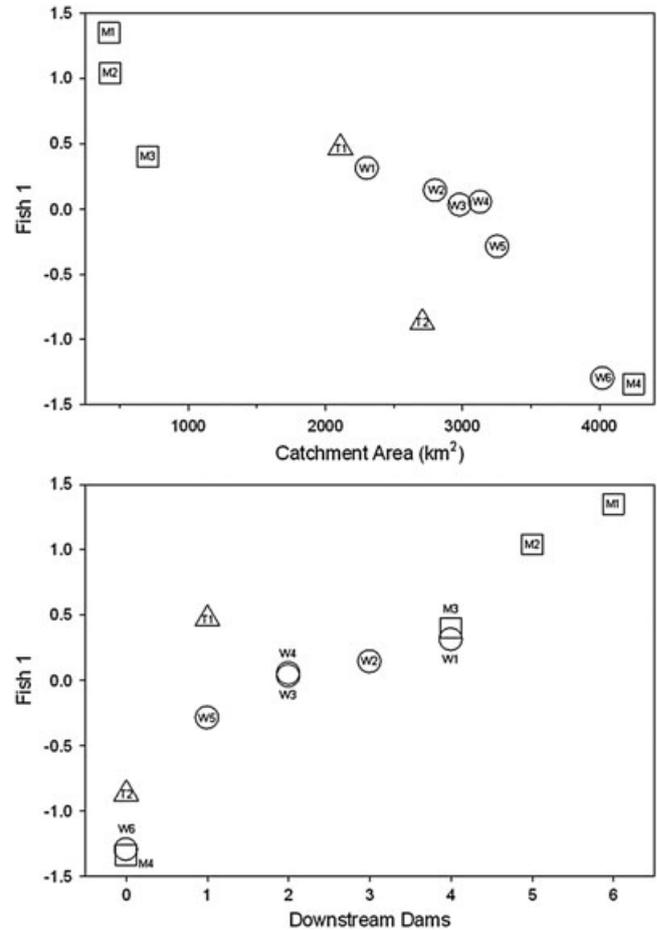


Figure 6. Relationships of Fish 1 axis scores with catchment area (top) and the number of downstream dams (bottom) in 12 reaches in three eastern Iowa rivers. Reaches are identified as in Figure 4

support greater abundance of certain species than shallower areas (Gerking, 1949; Aadland, 1993), are preferred to shallower areas by a number of species and life stages (Moyle and Baltz, 1985; Bisson *et al.*, 1988; Paragamian, 1989; Lobb and Orth, 1991; Aadland, 1993; Gelwicks, 2007), and offer greater refuge from avian predators (Power, 1984; Lonzarich and Quinn, 1995) than shallower areas. Studies in Iowa rivers have shown that deeper areas are preferred by both walleye (Paragamian, 1989) and channel catfish (Gelwicks, 2007) at certain times of the year. Despite previous demonstrations of the importance of deep areas in rivers, our results provided scant evidence of effects of depth and pool characteristics on fish assemblages as a whole at the reach scale. Fish assemblages in the Turkey River reaches were quite different from reaches in the other two rivers, and their low depth variation and large distances between pools were related to this difference. The presence of a few species was related to thalweg depth and pool characteristics. Mean thalweg depths were greater in reaches where two game fish species, channel catfish and white bass,

Table III. Mean physical, thalweg depth and pool characteristics that differed significantly between reaches where species were present or absent in three eastern Iowa rivers. Scientific names and other information for species are given in Table II

Characteristic	Species	Mean (standard deviation) where species is	
		Present	Absent
Catchment area (km ²)	Bigmouth buffalo	3022 (1155)	1594 (1090)
	Black buffalo	3802 (592)	1968 (1142)
	Bluegill	2085 (1138)	4137 (158)
	Bluntnose minnow	2085 (1138)	4138 (158)
	Bullhead minnow	3190 (710)	1358 (1213)
	Central stoneroller	1485 (1100)	2898 (1180)
	Channel catfish	2908 (1030)	985 (973)
	Common shiner	1639 (1079)	3529 (568)
	Highfin carpsucker	2828 (1004)	424 (6)
	Shorthead redhorse	2829 (1004)	425 (6)
	Smallmouth buffalo	3844 (520)	1955 (1125)
Sinuosity	Banded darter	1.85 (0.44)	1.51 (0.10)
	Emerald shiner	1.81 (0.40)	1.48 (0.08)
	River carpsucker	1.78 (0.37)	1.46 (0.06)
	Stonecat	2.23 (0.52)	1.53 (0.10)
Slope (%)	Emerald shiner	0.049 (0.011)	0.032 (0.005)
	River carpsucker	0.047 (0.011)	0.031 (0.005)
	White bass	0.054 (0.010)	0.034 (0.006)
Downstream dams	Emerald shiner	1.0 (1.5)	3.7 (1.6)
	Freshwater drum	0 (0)	3.1 (1.8)
	Gizzard shad	0 (0)	3.1 (1.8)
	Highfin carpsucker	1.7 (1.6)	5.5 (0.7)
	Hornyhead chub	4.7 (1.2)	1.6 (1.7)
	Redfin shiner	0.5 (0.6)	3.3 (1.9)
	River carpsucker	1.3 (1.6)	3.8 (1.8)
	River shiner	0.3 (0.6)	3.0 (1.9)
	Sauger	0 (0)	3.1 (1.8)
	Shorthead redhorse	1.7 (1.6)	5.5 (0.7)
	Shovelnose sturgeon	0 (0)	3.1 (1.8)
	Smallmouth buffalo	0.3 (0.6)	3.0 (1.9)
	Channel catfish	5.2 (2.0)	3.1 (0.7)
Maximum depth (m)	White bass	6.3 (2.5)	3.9 (1.1)
	Creek chub	28.5 (5.4)	55.6 (13.9)
Depth coefficient of variation	Orangespotted sunfish	42.2 (14.7)	61.9 (15.3)
	Fantail darter	0.1 (0.1)	7.3 (6.5)
Pool percentage of reach	Creek chub	0.38 (0.23)	1.66 (1.32)
Pool density (number/km)	Fantail darter	0.26 (0.12)	1.55 (1.28)
	Fantail darter	6.9 (6.9)	51.4 (40.9)
Mean pool length (m)	Hornyhead chub	89.6 (60.4)	28.8 (18.7)
	Creek chub	90.8 (18.1)	133.6 (31.0)
Pool length coef. of var.	Fantail darter	83.3 (17.8)	130.8 (30.5)
	River shiner	90.9 (18.3)	133.6 (31.0)
	Fantail darter	4393 (1669)	787 (556)
Mean inter-pool distance (m)			

were present, corroborating previous findings that deep areas are important to these species (McMahon and Terrell, 1982; Hamilton and Nelson, 1984; Aadland, 1993; IAGFA, 2005; Gelwicks, 2007). Pools were smaller and less prevalent on reaches where fantail darter and creek chub were present, which is consistent with their propensity towards occupying shallow areas (McMahon, 1982; IAGFA, 2005).

Longitudinal changes along the course of rivers are well-documented and are the foundation for a major body of

theory in river science (Vannote *et al.*, 1980; Johnson *et al.*, 1995). Many physicochemical characteristics change as rivers flow from headwaters to the sea (Leopold, 1994; Allan and Castillo, 2007). Longitudinal changes in fish assemblage structure were first described decades ago (Huet, 1959; Kuehne, 1962) and remain important both in understanding the ecology of rivers and in managing their biota and health (Oberdorff *et al.*, 1995; Matthews, 1998; Simon, 1999). Recent studies in China (Fu *et al.*, 2003),

France (Grenouillet *et al.*, 2004) and in Western (McGarvey and Hughes, 2008), Southern (McGarvey, 2011) and Midwestern United States (Chick *et al.*, 2006) demonstrate similar patterns of fish assemblage change along the course of rivers. Recent studies in Iowa (Wilton, 2004; Rowe *et al.*, 2009a; Neebling and Quist, 2010) document fish assemblage changes along longitudinal and stream size gradients consistent with patterns documented elsewhere. In our study, fish assemblages varied strongly with catchment area. The Fish 1 ordination axis scores of reaches in each of the three rivers arrayed in a similar pattern in relation to catchment area, reflecting similar patterns of species change from upstream to downstream. Black bullhead, rainbow darter, bluegill, bluntnose minnow, central stoneroller and common shiner tended to occur in upper reaches with small catchment areas and were found in few or no lower reaches. Bigmouth buffalo, black buffalo, emerald shiner, flathead catfish, freshwater drum, gizzard shad, sauger, shovelnose sturgeon and smallmouth buffalo showed the opposite longitudinal distribution, tending to occur in lower reaches with larger catchment areas and few or no upper reaches. These tendencies are consistent with previous reports of their distributions in Iowa and elsewhere (IAGFA, 2005). Neebling and Quist's (2010) study is the most comparable with our study and they found similar distributional patterns. They distinguished two fish assemblage types on several Iowa rivers tributary to the Mississippi River, and in most cases, their 'Mississippi A' assemblages were found in upper reaches (fifth order) and their 'Mississippi B' assemblages were found in lower reaches (sixth and seventh orders). The species occurring primarily in upper reaches in our study occurred in many of Neebling and Quist's Mississippi A reaches but sporadically in Mississippi B reaches. Likewise, the species occurring primarily in lower reaches in our study occurred in most of Neebling and Quist's Mississippi B reaches—especially those that were located in lower reaches of their study rivers but sporadically in Mississippi A reaches.

Alteration by dams has been shown to have numerous deleterious effects on rivers and their biota (Dynesius and Nilsson, 1994; Rosenberg *et al.*, 2000). Dams inundate riverine habitats (Benke, 1990), alter natural thermal regimes (Baxter, 1977), alter hydrologic and hydraulic regimes (Graf, 1999; Vörösmarty and Sahagian, 2000), disrupt natural sediment dynamics (Ligon *et al.*, 1995), alter energy availability and utilization (Ward and Stanford, 1979; Power *et al.*, 1996) and block upstream–downstream passage of fish and other biota (Pringle *et al.*, 2000). A study of 200 sites throughout Japan documented significant truncation of native species' ranges and invasion of impounded reaches by non-native species resulting from dams (Han *et al.*, 2008). Numerous studies have documented negative effects of dams on fish in Midwestern rivers. Blockage of fish passage by dams and similar structures has been demonstrated in several studies

(Pellett *et al.*, 1998; Santucci *et al.*, 2005; Butler and Wahl, 2011; Thomas *et al.*, 2011), with some illustrating how fragmentation of rivers resulted in truncated distributions and degraded fish assemblages (Santucci *et al.*, 2005; IDNR, 2010; Gelwicks and Steuck, 2011; Thomas *et al.*, 2011; Wang *et al.*, 2011). In a review of conservation status of catostomids, Cooke *et al.* (2005) listed migration barriers as the greatest threat to catostomid conservation in Midwestern rivers. In our study, fish assemblages varied strongly with the number of downstream dams. The Fish 1 ordination axis scores of reaches in each of the three rivers arrayed in a similar pattern in relation to number of downstream dams, reflecting similar patterns of species change as the number of barriers to downstream movement increased. Three species, common shiner, hornyhead chub and rainbow darter, showed a tendency towards the presence in upper reaches isolated from the Mississippi River by several dams and absence from lower reaches with few or no isolating dams. Many more species, including bigmouth buffalo, black buffalo, bowfin, burbot, crystal darter, emerald shiner, freshwater drum, gizzard shad, highfin carpsucker, longnose dace, longnose gar, Mississippi silvery minnow, mooneye, redbfin shiner, river carpsucker, river shiner, sauger, shoal chub, shorthead redhorse, shortnose gar, shovelnose sturgeon, silver chub and smallmouth buffalo, showed the opposite tendency towards presence in lower reaches with few or no isolating dams and absence in upper reaches isolated from the Mississippi River by dams. Blockage of fish passage, preventing re-colonisation from species-rich waters downstream and impeding seasonal downstream migrations of some species, loss of upstream riverine habitat due to inundation and downstream habitat alteration are all potential explanations for the orderly gradient in fish assemblages along the gradient of downstream dams. Santucci *et al.* (2005) found similarly downstream-truncated distributions in the Fox River, Illinois, for several of the species listed earlier, including bigmouth buffalo, black buffalo, gizzard shad, highfin carpsucker, longnose gar, mooneye, river carpsucker, sauger, shortnose gar and smallmouth buffalo, and attributed the upstream absence of these species to a series of dams blocking re-colonisation. The Upper Mississippi River System supports at least 122 fish species, 74 having been reported from Pool 13 (Barko *et al.*, 2005), including all of the species restricted to lower reaches in our study with the exceptions of crystal darter, longnose dace and shoal chub, which have been reported in other portions of the Mississippi River bordering Iowa (IAGFA, 2005). Isolation from this rich source of species for re-colonisation following floods, droughts and human-induced stresses seems a plausible explanation for the pattern we observed.

Our inverse relationships of catchment area and downstream dams with fish assemblage change begs the question of which relationship is more likely the primary one. Or in other words, which relationship is more likely reflective of

the ultimate cause or causes? Both patterns are supported with voluminous literatures, and each is an example of long-debated, competing paradigms regarding the structure and function of river ecosystems (Vannote *et al.*, 1980; Ward and Stanford, 1983) and their implications for fishes (Jungwirth *et al.*, 2000; Roberts and Hitt, 2010). The answer probably lies somewhere in the middle, with some of the assemblage differences reflecting natural distributional tendencies of species and some of the differences reflecting the effects of dams. Without an undammed reference stream for comparison, it is impossible to partition the effects with certainty. Clavero *et al.* (2004) reported a significant influence of dams on fish assemblages in rivers in Spain but acknowledged that it was not possible to separate effects of basin size. Wang *et al.* (2011) also acknowledged this conundrum in their analysis of the effects of dams and other factors on fish assemblages in rivers in Wisconsin and Michigan. They found a significant relationship of downstream dams and fish assemblages as we did, but even more variation in fish assemblage metrics was explained by river size and other environmental factors. They concluded that although the fraction of variance explained by dams was relatively small (<20%), it should not be surprising considering the many natural factors (e.g. zoogeography, river size and temperature) plus other anthropogenic factors (e.g. agriculture, logging and urbanisation) at work that may be influencing rivers and their fish assemblages. Evidence from dam removals (Kanehl *et al.*, 1997; Doyle *et al.*, 2005) strongly suggests that dams have profound effects on all aspects of the rivers they span, and widespread dam mitigation including removals is now underway in Iowa (IDNR, 2010).

The fish assemblage similarities within ecoregions that were evident in our ordination are probably because of a combination of ecoregional effects, within-river similarities and other confounding influences. The lower reaches of the Maquoketa and Wapsipinicon Rivers had very similar fish assemblages, and although both were the only reaches on their respective rivers in the RLP ecoregion, their similarity may be as much a reflection of similarly large catchment areas and lack of downstream dams than their shared ecoregion. Likewise, the loose similarities evident among the other Maquoketa and Wapsipinicon reaches might also be explained by catchment area and downstream dam effects. Assemblages in the Turkey River differed substantially from the other rivers and from each other, and these differences probably reflect both ecoregional effects and catchment area and downstream dam effects. Ten species, including fantail darter, black bullhead, burbot, crystal darter, longnose dace, longnose gar, mimic shiner, Mississippi silvery minnow, mooneye and shoal chub occurred only in Turkey River reaches. Fantail darter were found in both Turkey River reaches, black bullhead only in the upper reach

and the remaining eight species were found only in the lower reach. Five of these eight species are considered sensitive (Wilton, 2004) and three of these plus two others are SGCN (Zohrer, 2005). The lower Turkey River reach was an interesting case, supporting a unique fish fauna representing several downstream-distributed species found in the lower reaches of all three rivers plus some species usually associated with smaller streams and coarse substrates and several sensitive species and SGCN. The fish assemblage of the lower Turkey River reach appears to reflect both the well-documented influence of the PP ecoregion (Wilton, 2004; Heitke *et al.*, 2006; Rowe *et al.*, 2009a) and the proximity and free access to the large Mississippi River species pool.

The collective evidence to date from our study and many previous studies from both the Midwest and worldwide suggests that the pervasiveness of dams on rivers significantly alters fish assemblages, making underlying patterns of species change and relationships with naturally varying and human-influenced physical characteristics along a river's course difficult if not impossible to discern. Although we found few strong relationships of fish assemblages with thalweg depth and pool characteristics, we speculate that depth conditions are indeed important to many fish species in our study rivers as has been shown elsewhere, and our lack of relationships was at least in part a function of our spatial and temporal scales of resolution. A continuous sampling technique for the fish assemblage to match our continuous depth sampling, as has been demonstrated by Fausch *et al.* (2002) and Torgersen *et al.* (2006) might be more likely to identify depth relationships at the scale at which they actually occur. The strongest fish associations demonstrated to date with deep water in Iowa rivers have occurred in winter (Paragamian, 1989; Gelwicks, 2007), and thus, our summer and fall fish collections and the spatial scale of our analysis may have missed the relationships wintertime collections and a finer scale of resolution might have revealed. We believe that expanding previous fish sampling programs in rivers to a continuous spatial scale and including seasonal differences will help future studies further clarify the influence of physical and depth-related factors on fish assemblages.

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5476-I. The use of trade names or products does not constitute endorsement by the US Government.

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