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ANTHROPOGENIC DISTURBANCE AND ENVIRONMENTAL ASSOCIATIONS WITH FISH ASSEMBLAGE STRUCTURE IN TWO NONWADEABLE RIVERS

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ABSTRACT

Nonwadeable rivers are unique ecosystems that support high levels of aquatic biodiversity, yet they have been greatly altered by human activities. Although riverine fish assemblages have been studied in the past, we still have an incomplete understanding of how fish assemblages respond to both natural and anthropogenic influences in large rivers. The purpose of this study was to evaluate associations between fish assemblage structure and reach-scale habitat, dam, and watershed land use characteristics. In the summers of 2011 and 2012, comprehensive fish and environmental data were collected from 33 reaches in the Iowa and Cedar rivers of eastern-central Iowa. Canonical correspondence analysis (CCA) was used to evaluate environmental relationships with species relative abundance, functional trait abundance (e.g. catch rate of tolerant species), and functional trait composition (e.g. percentage of tolerant species). On the basis of partial CCAs, reach-scale habitat, dam characteristics, and watershed land use features explained 25.0–81.1%, 6.2–25.1%, and 5.8–47.2% of fish assemblage variation, respectively. Although reach-scale, dam, and land use factors contributed to overall assemblage structure, the majority of fish assemblage variation was constrained by reach-scale habitat factors. Specifically, mean annual discharge was consistently selected in nine of the 11 CCA models and accounted for the majority of explained fish assemblage variance by reach-scale habitat. This study provides important insight on the influence of anthropogenic disturbances across multiple spatial scales on fish assemblages in large river systems. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS: fish assemblage structure; longitudinal patterns; discharge; dams

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INTRODUCTION

Large rivers are characterized by high levels of fish and habitat diversity, yet they are also the focus of intense human activity (Karr *et al*., 1985; Hughes *et al*., 2005). The current status of riverine fish assemblages across North America can be generally considered poor (Rinne *et al*., 2005; Jelks *et al*., 2008; Burkhead, 2012). In general, lotic fish fauna in the central regions of the USA have experienced numerous declines, primarily because of anthropogenic alterations to rivers and their surrounding landscape (Karr *et al*., 1985; Hughes *et al*., 2005). To improve the conservation status of riverine fishes, it is critical to understand how fishes are influenced by dynamic river environments (Sparks, 1995; Hughes *et al*., 2005). Unfortunately, there is still an incomplete understanding about large-river ecology and how large-river ecosystems respond to anthropogenic disturbance (Johnson *et al*., 1995; Sparks, 1995; Allan, 2004). Historically, research on fishes in lotic systems has focused on wadeable streams because of the ease of sampling fishes in small streams compared with large, nonwadeable rivers (Johnson *et al*., 1995; Flotemersch *et al*., 2006). However, recent research on measurements of large-river biotic integrity (Lyons *et al*., 2001), sampling methodologies (Herzog *et al*., 2005; Flotemersch *et al*., 2006), and numerous efforts to model environmental relationships with fishes (Weigel *et al*., 2006; Neebling and Quist, 2010) have improved our understanding of fish ecology and management of nonwadeable rivers. Because of the widespread influence of human activities associated with the decline of riverine fish species, understanding the relationships between fishes and environmental factors in rivers is critical (Johnson *et al*., 1995; Allan, 2004; Hughes *et al*., 2005; Jelks *et al*., 2008).

Lotic systems, particularly in the Midwest, have a long history of disturbance and degradation from cumulative human activities (Karr *et al*., 1985). Anthropogenic activities such as land use (e.g. agricultural, urban, and industrial land use), channel modification, water development (e.g. dams, reservoirs, and levees), pollution, and the introductions of non-native species have been attributed to the decline of native fish assemblages and reduction of habitat quantity and quality in rivers throughout the Midwest (Rinne *et al*., 2005).

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In Iowa and much of the Midwest, agricultural and urban watershed land use are important sources of pollution, sedimentation, and hydrologic disturbance in streams, all of which have been attributed to biological impairment (Wang *et al*., 1997; Heitke *et al*., 2006; Rowe *et al*., 2009). Although urban and agricultural land uses are common alterations in watersheds, dams are considered one of the most pervasive disturbances affecting lotic ecosystems (Dynesius and Nilssen, 1994; Ward and Stanford, 1995). Dams can alter natural flow regimes (Poff and Allan, 1995; Poff *et al*., 1997), transform habitats immediately upstream and downstream of dams, and cause shifts in species composition (Quist *et al*., 2005; Chick *et al*., 2006) and trophic and spawning guild structure (Kinsolving and Bain, 1993; Guenther and Spacie, 2006). Dams can also influence fish assemblages in river reaches not in the immediate vicinity of dams or impoundments (Kinsolving and Bain, 1993; Falke and Gido, 2006; Weigel *et al*., 2006; Wang *et al*., 2011). One of the most notable effects of dams is how dams fragment habitat and limit the dispersal and distribution of fishes (Freeman *et al*., 2003; Santucci *et al*., 2005; Pierce *et al*., 2013). Previous studies on human disturbance in small lotic systems in the Midwest (Karr *et al*., 1985, Hughes *et al*., 2005) have made it apparent that fish assemblages and habitats have been long affected by watershed land use and water development.

Fish assemblage structure is governed by processes and habitat across multiple spatial and temporal scales. At a local scale, elements of the flow regime (Poff *et al*., 1997; Pyron and Lauer, 2004), channel morphology and geomorphic factors (Peterson and Rabeni, 2001; Pierce *et al*., 2013), substrate composition, instream cover, and bank condition have shown to be determinants of taxonomic and functional patterns exhibited by riverine fishes (Eitzmann and Paukert, 2010; Neebling and Quist, 2010). Components of local habitat tend to vary longitudinally and are reflected in broad patterns of fish assemblage structure (Vannote *et al*., 1980; Junk *et al*., 1989; Matthews, 1998; McGarvey and Ward, 2008; McGarvey, 2011). Spatial differences in habitat and fish assemblages become more apparent and complex when the flow regime is considered (Roberts and Hitt, 2010; Hitt and Roberts, 2012). For instance, upstream habitats tend to have greater flow variability than downstream environments (Schlosser, 1990; Poff *et al*., 1997). Depending on the degree of spatiotemporal variability exhibited by the river environment, fish life history and other functional trait variation can correspond strongly to these environmental patterns (Schlosser, 1990; Poff, 1997; Mimms and Olden, 2012). Human disturbances like dams and land use can disrupt longitudinal patterns in habitat conditions and fish assemblage structure (Chick *et al*., 2006; Miranda *et al*., 2008; McGarvey, 2011), artificially increase hydrologic variability in the environment (Poff and Allan, 1995), or even homogenize habitat (Poff *et al*., 1997). The influence of land use (Heitke *et al*., 2006; Rowe *et al*., 2009) and disturbance from dams (Gelwicks, 2007; Pierce *et al*., 2013) in Iowa has been partially disentangled from the effects of local habitat on lotic fishes in small streams, but the relative influence of disturbance and local habitat on fish assemblages remains relatively unknown in Iowa's large rivers.

The purpose of this study was to evaluate relationships between fish assemblage structure and environmental characteristics in two large nonwadeable rivers in Iowa. We sought to describe these relationships and compare the relative influence of watershed land use, dams, and reach-scale habitat factors on fish assemblage structure. To accomplish this objective, fish and environmental data were collected from the Cedar and Iowa rivers. Species-level descriptors and functional or autoecological traits (e.g. life history strategies and habitat use guilds) were used to describe structural associations between fish assemblages and environmental factors. We expected that variation in fish assemblages would be explained by both reach-scale habitat and watershed characteristics. In addition, we hypothesized that factors related to dams would explain as much or more of the variation in fish assemblage structure than land use features.

METHODS

Study area and survey design

This study was conducted in the Cedar and Iowa rivers, located within the upper Mississippi River basin of eastern-central Iowa. These two nonwadeable rivers flow northwest to southeast and altogether drain about a third of Iowa (32 430 km^2). The Cedar and Iowa rivers eventually meet and flow together for about 45 km to their confluence with the Mississippi River (Figure 1). During the summers of 2010 and 2011, data on fish and local habitat characteristics were collected from 33 mainstem sampling reaches (18 reaches in the Cedar River and 15 reaches in the Iowa River; Figure 1). Sampling reaches in both rivers were located upstream of the confluence of the Cedar and Iowa Rivers. To adequately describe the spatial distribution of fish species and environmental gradients along a river profile, sampling reaches were systematically established every 36–40 km along the entire length of each river. On the basis of the portion of each river considered to be nonwadeable (fourth to eighth Strahler stream order) and sampling logistics, 22 sampling reaches (each ~4 km in length) were systematically established in the Cedar and Iowa Rivers. Eleven additional sampling reaches were randomly placed 0–10 km upstream (reservoir environments were not sampled) or downstream of dams to further assess the influence of dams on fish assemblages.

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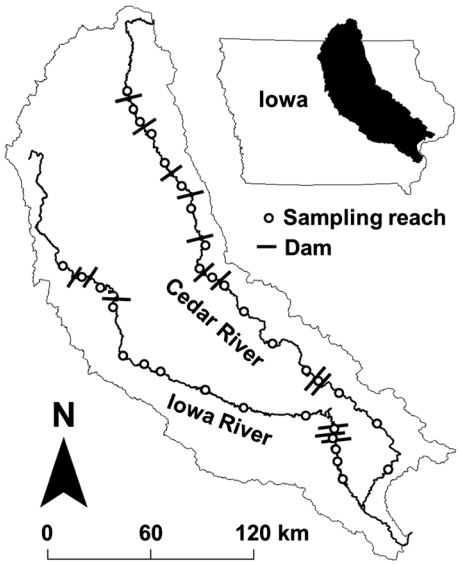

Figure 1. Map of 33 reaches where fish and reach-scale habitat were sampled along the Cedar and Iowa Rivers, Iowa, during 2010 and 2011

Fish assemblages

Fish assemblages were sampled using boat-mounted electrofishing and benthic trawling methods following the methods of Neebling and Quist (2010). At each reach, five 500-m boat-mounted electrofishing runs (2500 m total distance) were randomly established between 14 sections (each 100 m in length) reserved for 42 trawl runs. Three trawl runs (each 50 m in length) were performed in the channel in each 100-m section of the river. Boat-mounted electrofishing was performed during daytime hours in a downstream direction using a VVP-15B (Smith-Root Inc., Vancouver, WA, USA). Direct current was pulsed at 40–60 Hz, and power output was standardized to 3000 W. Boat-mounted electrofishing was performed with an operator and two netters using dip nets (6.3 mm delta, knotless mesh). Electrofishing was used to sample fish in a variety of habitats along the channel border. Trawling was performed during the day by hauling Herzog-Missouri trawls in a downstream direction at velocities slightly faster than the river current. Trawls sampled fish in benthic habitats in the thalweg and along its outer margins. Herzog-Missouri trawls were towed with 21.7-m-long towlines that provided a 7:1 m drop ratio (maximum depth = 3.1 m). Herzog-Missouri trawls have a larger (34.9-mm bar) outer mesh and a smaller (6.3 mm delta, knotless) inner mesh to efficiently sample both small-bodied and large-bodied fishes. Design and operation of Herzog-Missouri trawl can be found in the work of Herzog *et al.* (2005). Effort for each sampling run was recorded as time electrofished (hours) and distance trawled (metres). After each electrofishing or trawling run, sampled fishes were identified to species and enumerated. Unidentified specimens, as well as voucher specimens, were euthanized with MS-222 and preserved in 10% formalin.

Environmental data

Local environmental characteristics were measured and summarized at each fish sampling reach following Neebling and Quist (2010) who adapted methods used in the US Environmental Protection Agency's nonwadeable river protocol (Flotemersch *et al.*, 2006) and the Iowa Department of Natural Resources (DNR) wadeable streams physical habitat assessment (Wilton, 2004). Habitat measurements described channel geomorphology, substrate composition, instream cover, and bank and riparian characteristics. Reach-scale habitat was sampled along 20 evenly spaced transects between the borders of each fish sampling reach. At each transect, bankfull width (m) was measured using a digital rangefinder. Depth (m), current velocity ($m\,s^{-1}$), substrate composition, and instream cover were measured at seven evenly spaced locations along each transect. Depths were measured to the nearest decimetre using a sounding pole. Depths were taken at permanent physical references (e.g. bridge pylon) during fish sampling events to account for changes in river stage occurring between fish sampling and habitat sampling events. Substrate composition was estimated as the percentage of clay and silt (≤0.06 mm), sand (0.07–2 mm), gravel (3–64 mm), cobble (65–255 mm), boulder (≥256 mm), or bedrock (Orth and Maughan, 1982). Current velocity ($m\,s^{-1}$) was measured at each of the seven transect locations using a Marsh-McBirney Flow-Mate 2000 (Marsh-McBirney Inc., Loveland, CO, USA). At each location, current velocity was measured at 20% and 80% of the depth when depth ≥ 1.0 m and at 60% when depth < 1.0 m (Fitzpatrick *et al.*, 1998). Visible instream cover (large woody debris, vegetation, rock debris, and artificial debris) was measured as the per cent of instream cover along the length of the river transect. Canopy cover and bank condition were measured at the endpoint of each transect. Canopy cover, expressed as an aerial percentage of the overhanging canopy, was measured facing the bank at each transect using a spherical densiometer. Bank condition was measured as the percentage of shoreline rocky rip-rap in each reach (Eitzmann and Paukert, 2010). The length of downstream shoreline rip-rap was measured to the nearest 0.5 m using a digital rangefinder (maximum length of 200.0 m per bank). Conductivity ($\mu S\,cm^{-1}$) was measured before and after electrofishing runs using an EC400 ExStik II conductivity meter (Extech Instruments, Nashua, NH, USA). Streamflow conditions, describing flow magnitude and variability, were quantified as mean annual discharge ($m^3\,s^{-1}$) and the coefficient of variation of annual discharge values (hereafter referred to as the annual discharge CV), respectively. Mean annual discharge and the annual discharge CV values were calculated using Indicators of Hydrologic Alteration (Richter *et al.*, 1996) with 20 years of available daily flow data (1990–2011; 20 water years) from 12 US Geological Survey (USGS) gauging stations. Mean annual discharge

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values were interpolated for all study reaches using the drainage area upstream of each site. Annual discharge CV values were used to generally describe the overall spatial pattern of flow variation and were not included in further analyses. Variables associated with dams were derived using a geographical information system (GIS; ArcGIS 9.3, ESRI, Redlands, CA, USA). Data on dams were obtained from a state dam inventory layer available from the Iowa DNR GIS library (IDNR, 2004). Dam locations were superimposed over a map layer of river and stream networks sourced from a 1:100 000 scale National Hydrography Dataset (NHD; USGS, 2004). Spatial characteristics of dams were similar to those in the works of Weigel *et al*. (2006) and Wang *et al*. (2011), where the effects of dams were characterized relative to the network position of each fish sampling reach. Distance (rkm) to upstream dam and distance to downstream dam impoundment were determined for each fish sampling reach. To quantify fragment size, mainstem channel length (rkm) free of dams was measured for each sampling reach (i.e. sum of reach distance to upstream dam and distance to downstream dam impoundment; Perkin and Gido, 2011).

Land cover characteristics were also analysed using a GIS to describe land use percentages within local catchments and basins. Methods similar to that of Rowe *et al*. (2009) were employed to determine catchment areas and land cover percentages. Basins (i.e. network catchments) were defined as the total upstream watershed area draining into each sampling reach. Basins describe the cumulative influence from the landscape encompassing a river network, upstream of each sampling reach. Local catchment areas were defined as a river's lateral drainage area confined by the upstream and downstream boundaries of each sampling reach and by the drainage boundaries determined by river network (i.e. catchment boundaries set by the NHD from digital elevation models). Local catchments describe the immediate landscape (i.e. riparian and valley area) that contributes runoff along the length of the sampling reach. A digital elevation model (30-m resolution) joined to a 1:100 000 scale NHD coverage was used to delineate basin and local catchment areas using Arc Hydro tools (available in ArcGIS 9.3, ESRI, Redlands, CA). Land cover raster data (2006 National Land Cover Dataset; Fry *et al*., 2011) were superimposed onto catchment delineations to calculate land use percentages. A suite of natural and anthropogenic land cover variables were derived for each catchment including per cent agricultural, urban, grassland, wetland, and forest land cover.

Data analysis

Fifty-four candidate environmental variables (26 reach-scale, 7 dam-related, and 16 land use variables) were initially considered for investigation, but the number was reduced to avoid issues of multicollinearity. Pearson's correlation coefficients were calculated for all pairs of environmental variables to identify sources of redundancy among correlated variables. Highly correlated variables were considered to have a Pearson's $r \geq |0.70|$. An example of a variable that was redundant with other variables is mean annual discharge. Mean annual discharge was highly correlated with 10 variables, including basin drainage area; per cent grassland, forest, and wetland land use in basin catchments; per cent grassland and agricultural land use in local catchments; and the density and number of upstream and downstream dams. Consequently, mean annual discharge was retained. Because of all of the initial 54 variables were considered 'ecologically relevant', we retained as many variables as possible. Environmental variables were also reduced by aggregating correlated variables into composite variables. Composite variables such as per cent coarse substrate (i.e. substrates > 2 mm in diameter) and percentage of basin agricultural land use (i.e. row crop and pasture) were created to retain as much habitat information as possible. The final set of variables used in the analysis included 21 environmental variables that were not highly correlated with one another (i.e. $r \leq |0.70|$; Table I).

Fish assemblage structure was described using species relative abundance, and the relative abundance and richness measures of several functional trait classifications. Functional trait classifications included tolerance guilds (Wilton, 2004), life history strategies (Winemiller and Rose, 1992), and habitat use guilds (Kinsolving and Bain, 1993; Galat and Zweimuller, 2001). Tolerance guilds were defined as fish species tolerant, moderately tolerant, and intolerant of environmental degradation (Wilton, 2004). Fish life history strategies were classified using methods described by Olden and Kennard (2010) following the Winemiller and Rose (1992) life history model. Life history strategies typically have been used to describe a species response to disturbance and other hydrodynamic changes in the environment (Poff, 1997; Olden and Kennard, 2010; Mimms and Olden, 2012). Life history strategies were based on length at maturity, fecundity, ovum diameter, and parental care data from Becker (1983) and Carlander (1969, 1977, 1997). Using these life history traits, species were either classified by their primary affinity with a single life history strategy (e.g. periodic, opportunistic, or equilibrium) or by their intermediate affinity between two strategies (e.g. opportunistic–periodic; Hoeinghaus *et al*., 2007; Olden and Kennard, 2010). Habitat use guild classifications were defined as those fish species requiring free-flowing lotic habitats to complete all (i.e. fluvial specialists) or a portion of their life history (i.e. fluvial dependents), or fish species that generalize across habitats and are capable of completing their life history in lentic habitats (i.e. macrohabitat generalists; Kinsolving and Bain, 1993; Galat and Zweimuller, 2001).

Relative abundance was calculated as catch per unit effort (CPUE) by species and functional trait classification and was calculated separately for electrofishing and trawling

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Table I. Summarized reach, dam, and landscape environmental characteristics measured from 33 sites in the Cedar and Iowa Rivers, Iowa, during 2010 and 2011

Variable and description	Abbreviation	Mean	Standard deviation	Minimum	Maximum
Reach variables					
Mean annual discharge ($m^3 s^{-1}$)	Discharge	2106.00	1520.00	383.00	5135.00
Annual discharge coefficient of variation[a]	AnnualCV	1.47	0.26	2.00	1.15
Conductivity ($\mu S\,cm^{-1}$)	Cond	547.00	55.50	416.00	648.00
Mean bankfull width (m)	BFW	97.00	46.30	43.90	213.20
Mean depth (m)	Depth	1.29	0.48	0.61	2.55
Coefficient of variation of depth (%)	DepthCV	49.00	13.30	23.20	75.60
Mean current velocity ($m\,s^{-1}$)	Velocity	0.41	0.20	0.08	0.82
Coefficient of variation of current velocity (%)	VelocityCV	50.20	14.90	23.70	94.20
Per cent coarse substrate (>2 mm)	Coarse	23.58	19.80	0.00	83.40
Per cent overhanging canopy cover (mean % per reach)	Canopy	58.00	16.10	23.70	89.30
Per cent of shore length rip-rap (% length of upstream shoreline)	RipRap	10.73	12.90	0.00	49.87
Per cent of total instream cover (% of transect)	InstreamCover	18.25	3.50	9.44	27.22
Per cent of woody debris cover (% of transect)	WoodCover	12.78	5.03	0.04	21.11
Dam variables					
Distance to upstream dam (km)	DistUpDm	50.98	92.80	1.68	508.10
Distance to downstream dam or impoundment (km)	DstDnDm	58.02	63.20	0.01	198.48
Mainstem fragment length (km) between dams and impoundment boundaries	FragLength	128.23	122.00	5.52	510.62
Landscape variables					
Per cent of urban land use area in local catchment	LocUrb	17.74	23.60	0.70	94.60
Per cent of forested area in local catchment	LocFrst	10.04	15.90	0.00	69.35
Per cent of wetland area in local catchment	LocWet	22.00	23.80	0.26	77.90
Per cent of urban land use area in entire upstream catchment	BasinUrb	8.05	0.71	6.84	9.27
Per cent of agricultural land use area in entire upstream catchment	BasinAg	82.40	2.40	78.30	87.20

[a]Annual discharge coefficient of variation calculated by Indicators of Hydrologic Alteration as a dimensionless value. Additionally, the annual discharge coefficient of variation was only calculated for 12 US Geological Survey gauging stations to generally describe overall flow patterns and was not included in the analyses.

data. Electrofishing CPUE was calculated as the number of fish caught per hour of electrofishing ($fish\,h^{-1}$). Trawling CPUE was calculated as the number of fish caught per 50-m trawl haul. Additionally, fish assemblage structure was described by the percentage of species present representing a specific functional trait (Pool *et al*., 2010), hereafter referred to as per cent composition of functional traits. Per cent composition datasets were created for tolerance guilds, life history strategies, and habitat use guilds using species presence–absence data aggregated from electrofishing and trawling data.

Before multivariate analyses were performed, spatial patterns in species occurrence were screened to observe if dams were acting as possible barriers to fish movement. Dams can only be inferred as barriers when species distributions appear to be truncated (Santucci *et al*., 2005). Truncated species distributions were defined as species only occurring downstream of dams. Historical data from Loan-Wilsey *et al*. (2005) were used to confirm the validity of truncated species distributions.

Canonical correspondence analyses (CCAs) were performed to examine the relationships between fish assemblage structure (i.e. taxonomic and trait data) with environmental variables at multiple spatial scales. Count data were log transformed [$\log(x+1)$], and percentage data were arc-sine square root transformed to help meet assumptions of the model (Legendre and Legendre, 1998). Species occurring at less than three reaches (i.e. 10% of reaches) were excluded from analyses to reduce the influence of rare species (Legendre and Legendre, 1998). Separate CCAs were performed for electrofishing CPUE, trawling CPUE, and trait richness datasets. CCAs were conducted using a forward-selection procedure with Monte Carlo permutation tests (1000 permutations) to identify and retain environmental variables significantly ($p \leq 0.05$) explaining variation in fish assemblage structure among data sets (ter Braak and Smilauer, 2002). Variance inflation factors were assessed in each model to reduce the possibility of over-fitting the CCA models. Only environmental variables with variance inflation factors <10 were retained in CCA models (ter Braak and Smilauer, 2002). Environment–fish assemblage relationships were depicted in ordinations using the first two CCA ordination axes. In all cases, the third axis described a limited amount of model variance (≤10% of total variance).

Partial CCAs (pCCAs) were used to partition fish assemblage variation explained by groups of interrelated environmental variables. Specifically, pCCAs were used to determine the relative importance of reach-scale habitat, dam, and land

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use environmental variables (Pool *et al*., 2010; Wang *et al*., 2011). The pCCAs were performed by partitioning the total inertia (i.e. χ^2 distance) or total variance in fish assemblages constrained by each set of environmental variables in each of the previously created CCA models (Legendre and Legendre, 1998). The proportion of constrained inertia explained by each group of environmental characteristics was expressed as the percentage of explained assemblage variation (ter Braak and Smilauer, 2002). Similar to Pool *et al*. (2010) and Wang *et al*. (2011), percentages representing reach-scale, dam, and land use variables were graphically depicted for each CCA model to compare the relative importance of each set of environmental factors on fish assemblage characteristics. Additionally, we also assessed the percentages of assemblage variation explained by individual environmental variables to better understand the most likely environmental drivers of fish assemblage structure. All CCA ordinations and pCCA analyses were performed using the Vegan package in R (R Development Core Team, 2011).

RESULTS

During the summers of 2010 and 2011, 16,033 fish were sampled using boat-mounted electrofishing and 21,201 fish were sampled using benthic trawls in the Cedar and Iowa rivers. Gizzard shad *Dorosoma cepediamum* (3,229), spotfin shiner *Cyprinella spiloptera* (2,459), golden redhorse *Moxostoma erythrurum* (1,511), and common carp *Cyprinus carpio* (1,452) dominated the electrofishing catch. Sand shiner *Notropis stramineus* (8,834), bigmouth shiner *Notropis dorsalis* (1,686), channel catfish *Ictalurus punctatus* (3,763), and banded darter *Etheostoma zonale* (1,309) dominated samples with the trawl. Eighty-five species and two hybrids were sampled in total (Table II). Species richness varied from 18 to 43 species per reach in the Iowa River and 26 to 43 species per reach in the Cedar River (Figure 2, top panels). Although species richness did not change consistently with longitudinal position in either river, longitudinal variations in fish assemblages were apparent through patterns of trait composition (Figure 2, lower panels).

Abrupt shifts in species composition occurring in downstream river reaches appeared to characterize fragmentation from dams. Truncated distributions of several species occurred in river reaches below the furthest downstream dam in each river (Table III). Thirteen species were not sampled upstream of the Burlington Street Dam on the Iowa River, including shovelnose sturgeon *Scaphirhynchus platorynchus*, longnose gar *Lepisosteus osseus*, shortnose gar *Lepisosteus platostomus*, bowfin *Amia calva*, mooneye *Hiodon tergisus*, shoal chub *Macrhybopsis hyostoma*, emerald shiner *Notropis atherinoides*, river shiner *Notropis blennius*, mimic shiner *Notropis volucellus*, channel shiner *Notropis wickliffi*, blue sucker *Cycleptus elongatus*, western sand darter *Ammocrypta clara*, and sauger *Sander canadensis*. Similarly, eight species were not sampled upstream of the Cedar Rapids Milldam on the Cedar River including longnose gar, shortnose gar, goldeye *Hiodon alosoides*, mooneye, Mississippi silvery minnow *Hybognathus nuchalis*, silver chub *Macrhybopsis storeriana*, emerald shiner, and sauger.

Twenty-one of the fifty-four environmental variables were retained for analysis and varied among study reaches (Table I). Mean annual discharge ($2106 \pm 1520\,m^3\,s^{-1}$; mean ± standard deviation), bankfull width (97.0 ± 46.3 m), conductivity ($547.0 \pm 55.5\,\mu S\,cm^{-1}$), and per cent coarse substrate ($23.6 \pm 19.8\%$) exhibited the most inter-reach variation among reach-scale characteristics. Among the variables associated with dams, mainstem fragment length (128.2 ± 122.0 km), distance to upstream dam (51.0 ± 92.8 km), and distance to downstream dam impoundment (58.0 ± 63.2 km) varied among study reaches. Percentages of wetland cover ($22.0 \pm 23.8\%$), forest ($10.0 \pm 15.9\%$), and urban ($17.7 \pm 23.6\%$) land use in local catchments exhibited the most inter-reach variation among land use variables, whereas percentages of agricultural ($82.4 \pm 2.4\%$) and urban ($8.0 \pm 0.7\%$) land use measured at the basin scale were fairly constant. Several environmental characteristics exhibited some degree of longitudinal variation, including the percentage of basin agriculture, conductivity, canopy cover, mean bankfull width, and mean annual discharge; yet, no major correlation occurred among these variables ($r < |0.70|$). Similarly, indicators of hydrologic alteration analysis calculated annual discharge CV values, which exhibited a strong negative correlation ($r = -0.88$) with mean annual discharge at the USGS gauge locations, where upstream USGS gauges recorded greater flow variability over time (e.g. 05458500-Cedar River at Janesville, annual CV = 1.61; 05451500-Iowa River at Marshalltown, annual CV = 1.51) compared with the more stable flows recorded at downstream gauges (e.g. 05465000-Cedar River at Conesville, annual CV = 1.19; 05455700-Iowa River at Lonetree, annual CV = 1.18).

Taxonomic abundance models

Environmental characteristics explained slightly more variation in taxonomic abundance in the electrofishing CCA model (57.3% of total variance) than the trawling CCA model (53.3%; Figure 3). Forward selection retained seven environmental variables that significantly explained ($p < 0.05$, based on Monte Carlo simulations) patterns of species abundance in the electrofishing CCA. The positions occupied by species in ordination space described a longitudinal pattern in the distribution of species (left to right) along Axis 1. Axis 1 represented a gradient of discharge,

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Table II. Summary of per cent occurrence and mean (*SD*) catch rates for fish species sampled in the Iowa and Cedar Rivers, Iowa, during 2010 and 2011

			Iowa River ($n = 15$)			Cedar River ($n = 18$)		
Family and species	Scientific name	Abbreviation	Per cent	Electrofishing	Trawling	Per cent	Electrofishing	Trawling
Acipenseridae								
Shovelnose sturgeon[a]	*Scaphirhynchus platorynchus*	snsg	20	0.83 (3.06)	0.01 (0.03)	28	0.41 (1.03)	0.01 (0.02)
Lepisosteidae								
Longnose gar[a]	*Lepisosteus osseus*	lngr	13	0.26 (0.75)	0.00 (0.01)	17	0.80 (2.75)	0.00 (0.01)
Shortnose gar	*Lepisosteus platostomus*	sngr	20	2.86 (6.35)	—	17	2.12 (5.18)	0.00 (0.01)
Amiidae								
Bowfin[a]	*Amia calva*	bwfn	7	0.08 (0.29)	—	0	—	—
Hiodontidae								
Goldeye[a]	*Hiodon alosoides*	gdey	0	—	—	6	0.04 (0.16)	—
Mooneye	*Hiodon tergisus*	mney	7	0.11 (0.44)	0.00 (0.01)	11	0.23 (0.81)	—
Clupeidae								
Gizzard shad	*Dorosoma cepedianum*	gzsd	73	121.85 (273.53)	0.01 (0.03)	50	16.19 (38.12)	—
Cyprinidae								
Central stoneroller	*Campostoma anomalum*	cnsr	13	1.02 (2.98)	0.00 (0.01)	11	0.39 (1.45)	0.00 (0.01)
Goldfish[b]	*Carassius auratus*	gdfh	13	0.40 (1.40)	—	11	0.30 (0.90)	—
White amur[b]	*Ctenopharyngodon idella*	gscp	27	0.27 (0.50)	—	11	0.08 (0.26)	—
Spotfin shiner	*Cyprinella spiloptera*	sfsn	100	67.56 (77.45)	0.18 (0.25)	89	36.22 (39.37)	0.32 (0.37)
Common carp[b]	*Cyprinus carpio*	crap	100	33.32 (10.60)	—	100	29.14 (24.96)	—
Gravel chub[a]	*Erimystax x-punctatus*	gvcb	0	—	—	56	—	0.10 (0.17)
Brassy minnow	*Hybognathus hankinsoni*	bsmw	40	1.35 (3.01)	0.02 (0.03)	0	—	—
Mississippi silvery minnow[a]	*Hybognathus nuchalis*	svmw	0	—	—	6	—	0.00 (0.01)
Common shiner	*Luxilus cornutus*	cmsn	27	3.96 (9.59)	0.04 (0.13)	22	3.32 (7.58)	0.04 (0.15)
Shoal chub	*Macrhybopsis hyostoma*	skcb	20	—	0.15 (0.39)	44	—	0.36 (1.06)
Silver chub	*Macrhybopsis storeriana*	svcb	67	0.31 (0.60)	0.29 (0.28)	17	—	0.01 (0.01)
Hornyhead chub	*Nocomis biguttatus*	hhcb	27	1.22 (3.12)	0.03 (0.12)	39	5.72 (15.62)	0.08 (0.19)
Golden shiner	*Notemigonus crysoleucas*	gdsn	7	0.04 (0.16)	—	11	0.12 (0.37)	—
Emerald shiner	*Notropis atherinoides*	emsn	20	0.74 (2.07)	0.38 (1.41)	11	1.38 (4.64)	0.01 (0.04)
River shiner	*Notropis blennius*	rvsn	7	—	0.00 (0.01)	22	—	0.06 (0.16)
Bigmouth shiner	*Notropis dorsalis*	bmsn	80	3.60 (5.71)	1.85 (2.87)	50	2.83 (10.85)	0.67 (1.45)
Ozark minnow[a]	*Notropis nubilus*	ozmw	0	—	—	17	0.26 (0.80)	0.02 (0.08)
Rosyface shiner	*Notropis rubellus*	rysn	20	0.46 (0.96)	0.00 (0.01)	56	8.56 (16.08)	0.13 (0.31)
Sand shiner	*Notropis stramineus*	snsn	80	2.92 (4.35)	1.10 (1.39)	100	2.87 (4.94)	10.44 (15.10)
Mimic shiner	*Notropis volucellus*	mmsn	20	—	0.03 (0.08)	0	—	—
Channel shiner	*Notropis wickliffi*	cnsn	13	—	0.01 (0.04)	0	—	—
Suckermouth minnow	*Phenacobius mirabilis*	smmw	20	0.46 (1.21)	0.00 (0.01)	17	—	0.00 (0.01)
Southern redbelly dace[a]	*Phoxinus erythrogaster*	srbd	0	—	—	11	0.42 (1.63)	—
Bluntnose minnow	*Pimephales notatus*	bnmw	60	3.17 (6.50)	0.06 (0.16)	83	6.82 (11.57)	0.43 (0.78)
Fathead minnow	*Pimephales promelas*	fhmw	60	1.20 (1.61)	0.02 (0.03)	28	0.29 (0.54)	0.01 (0.03)
Bullhead minnow	*Pimephales vigilax*	bhmw	47	0.38 (0.71)	0.16 (0.30)	78	0.11 (0.35)	0.62 (0.86)
Blacknose dace	*Rhinichthys atratulus*	bndc	7	—	0.00 (0.01)	6	—	0.00 (0.01)
Creek chub	*Semotilus atromaculatus*	ckcb	7	—	0.00 (0.01)	22	0.26 (0.82)	0.00 (0.01)

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Table II. (Continued)

Family and species	Scientific name	Abbreviation	Iowa River ($n = 15$)			Cedar River ($n = 18$)		
			Per cent	Electrofishing	Trawling	Per cent	Electrofishing	Trawling
Catostomidae								
River carpsucker	*Carpiodes carpio*	rvcs	80	14.41 (13.80)	0.00 (0.01)	100	24.69 (25.04)	0.01 (0.02)
Quillback carpsucker	*Carpiodes cyprinus*	qbck	33	1.37 (3.16)	0.00 (0.01)	78	5.99 (10.39)	0.00 (0.01)
Highfin carpsucker	*Carpiodes velifer*	hfcs	40	2.04 (4.16)	—	83	11.23 (12.65)	—
White sucker	*Catostomus commersoni*	wtsk	27	2.65 (6.31)	0.02 (0.06)	50	8.53 (17.61)	0.25 (0.89)
Blue sucker[a]	*Cycleptus elongatus*	busk	7	0.04 (0.15)	—	28	0.16 (0.38)	0.00 (0.01)
Northern hog sucker	*Hypentelium nigricans*	nhsk	33	4.22 (10.58)	0.06 (0.17)	72	4.96 (7.82)	0.05 (0.06)
Smallmouth buffalo	*Ictiobus bubalus*	smbf	73	5.53 (5.47)	—	50	2.82 (3.45)	—
Bigmouth buffalo	*Ictiobus cyprinellus*	bmbf	60	2.80 (4.26)	—	61	2.22 (2.65)	0.00 (0.01)
Black buffalo[a]	*Ictiobus niger*	bkbf	60	4.77 (8.02)	0.00 (0.01)	28	0.88 (1.78)	—
Silver redhorse	*Moxostoma anisurum*	svrh	33	1.46 (3.15)	—	78	15.93 (15.92)	—
River redhorse[a]	*Moxostoma carinatum*	rvrh	20	0.70 (2.00)	—	44	0.95 (1.54)	—
Black redhorse[a]	*Moxostoma duquesnei*	bkrh	20	0.53 (1.38)	0.01 (0.01)	11	0.09 (0.26)	—
Golden redhorse	*Moxostoma erythrurum*	gdrh	60	25.90 (37.62)	0.06 (0.13)	89	42.77 (40.48)	0.22 (0.27)
Shorthead redhorse	*Moxostoma macrolepidotum*	shrh	93	20.08 (18.53)	0.04 (0.05)	100	31.94 (25.64)	0.02 (0.03)
Ictaluridae								
Black bullhead	*Ameiurus melas*	bkbh	13	0.38 (1.02)	0.02 (0.06)	0	—	—
Yellow bullhead	*Ameiurus natalis*	ywbh	7	0.69 (2.67)	—	0	—	—
Channel catfish	*Ictalurus punctatus*	cncf	93	7.22 (5.34)	3.53 (7.71)	83	4.11 (5.31)	1.84 (3.85)
Stonecat	*Noturus flavus*	stct	53	0.15 (0.40)	0.22 (0.70)	61	—	0.04 (0.05)
Tadpole madtom[a]	*Noturus gyrinus*	tpmt	0	—	—	17	—	0.00 (0.01)
Freckled madtom[a]	*Noturus nocturnus*	fkmt	27	0.04 (0.17)	0.03 (0.06)	6	—	0.01 (0.04)
Flathead catfish	*Pylodictis olivaris*	fhcf	67	7.31 (9.27)	0.01 (0.02)	39	2.48 (5.19)	0.00 (0.01)
Esocidae								
Northern pike	*Esox lucius*	ntpk	40	1.93 (3.29)	—	72	1.25 (1.47)	0.00 (0.01)
Fundulidae								
Blackstripe topminnow[a]	*Fundulus notatus*	bttm	0	—	—	6	0.08 (0.34)	—
Atherinopsidae								
Brook silverside	*Labidesthes sicculus*	bkss	0	—	—	6	0.04 (0.17)	—
Gasterosteidae								
Brook stickleback	*Culaea inconstans*	bksb	7	—	0.00 (0.01)	0	—	—
Moronidae								
White bass	*Morone chrysops*	wtbs	67	1.94 (2.39)	0.03 (0.06)	33	0.78 (1.62)	0.01 (0.02)
Striped bass × white bass[c]	*Morone saxatilis* × *Morone chrysops*	sbwb	7	0.21 (0.82)	—	0	—	—
Centrarchidae								
Rock bass	*Ambloplites rupestris*	rkbs	13	0.10 (0.27)	—	39	6.23 (15.68)	0.01 (0.02)
Green sunfish	*Lepomis cyanellus*	gnsf	53	2.34 (4.49)	—	67	2.04 (3.57)	0.00 (0.01)
Orangespotted sunfish	*Lepomis humilis*	ossf	33	0.35 (1.08)	0.00 (0.01)	11	—	0.00 (0.01)
Bluegill	*Lepomis macrochirus*	blgl	60	4.06 (5.87)	0.00 (0.01)	33	0.50 (1.19)	0.00 (0.01)
Bluegill × green sunfish[c]	*Lepomis macrochirus* × *Lepomis cyanellus*	bggs	27	0.28 (0.59)	—	11	0.08 (0.36)	0.00 (0.01)
Smallmouth bass	*Micropterus dolomieu*	smbs	80	4.25 (6.18)	0.01 (0.03)	100	14.10 (11.90)	0.06 (0.08)

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Table II. (Continued)

Family and species	Scientific name	Abbreviation	Iowa River ($n = 15$)			Cedar River ($n = 18$)		
			Per cent	Electrofishing	Trawling	Per cent	Electrofishing	Trawling
Largemouth bass	*Micropterus salmoides*	lmbs	27	1.76 (3.55)	—	28	0.33 (0.86)	0.00 (0.01)
White crappie	*Pomoxis annularis*	wtcp	27	0.17 (0.46)	0.02 (0.06)	17	0.07 (0.19)	0.00 (0.01)
Black crappie	*Pomoxis nigromaculatus*	bkcp	47	0.40 (0.55)	0.01 (0.02)	33	0.46 (0.89)	0.00 (0.01)
Percidae								
Western sand darter[a]	*Ammocrypta clara*	wsdr	**7**	—	0.00 (0.01)	50	—	0.06 (0.10)
Mud darter[a]	*Etheostoma asprigene*	mddr	27	—	0.01 (0.02)	0	—	—
Rainbow darter	*Etheostoma caeruleum*	rbdr	0	—	—	6	—	0.01 (0.05)
Iowa darter[a]	*Etheostoma exile*	iodr	13	—	0.01 (0.02)	0	—	—
Fantail darter	*Etheostoma flabellare*	ftdr	13	—	0.12 (0.37)	22	0.16 (0.41)	0.01 (0.03)
Johnny darter	*Etheostoma nigrum*	jydr	73	0.05 (0.21)	0.16 (0.47)	61	0.07 (0.21)	0.25 (0.43)
Banded darter[a]	*Etheostoma zonale*	bddr	7	0.14 (0.54)	0.16 (0.63)	39	0.05 (0.19)	1.59 (5.48)
Yellow perch	*Perca flavescens*	ywph	0	—	—	17	0.44 (1.36)	0.00 (0.02)
Logperch[a]	*Percina caprodes*	lgph	7	—	0.00 (0.01)	67	0.27 (0.52)	0.37 (0.77)
Blackside darter[a]	*Percina maculata*	bkdr	47	0.34 (0.90)	0.48 (0.82)	28	0.40 (1.08)	0.06 (0.13)
Slenderhead darter[a]	*Percina phoxocephala*	shdr	73	0.06 (0.22)	0.50 (1.27)	94	0.09 (0.39)	0.77 (1.07)
Sauger	*Sander canadensis*	sger	7	0.08 (0.29)	—	6	0.12 (0.50)	—
Walleye	*Sander vitreus*	wlye	73	1.53 (1.78)	0.04 (0.07)	83	3.66 (4.66)	0.06 (0.08)
Sciaenidae								
Freshwater drum	*Aplodinotus grunniens*	fwdm	40	0.61 (1.09)	0.02 (0.06)	44	1.13 (1.82)	0.00 (0.01)

Catch per unit effort was calculated as the number of fish per hour for electrofishing and number of fish per 50 m of trawling.
[a]Species of greatest conservation need in Iowa.
[b]Non-native.
[c]Hybrid.

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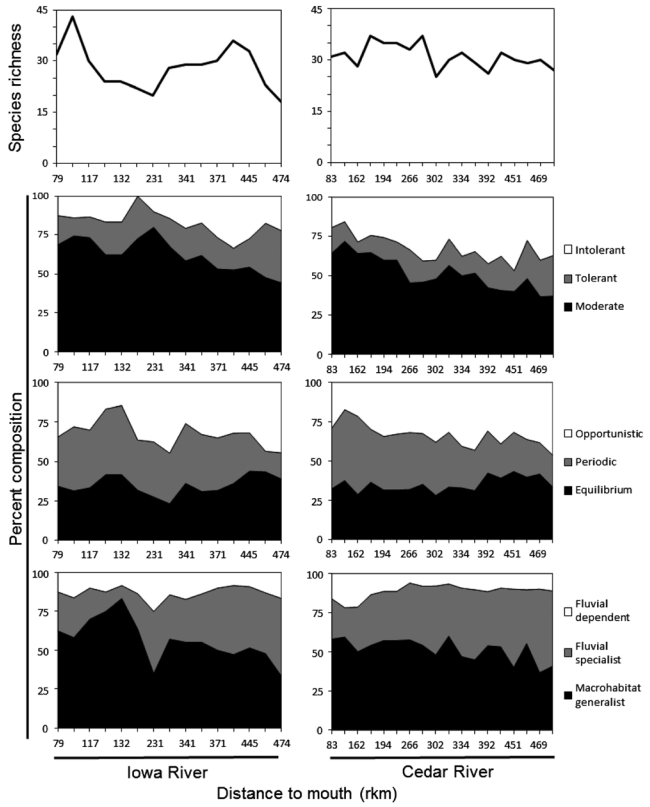

Figure 2. Species richness and per cent composition of tolerance traits, life history strategies, and habitat use guilds describing fish assemblages sampled from reaches distributed longitudinally along the Cedar and Iowa Rivers, Iowa, during 2010 and 2011

canopy cover, agricultural land use, and riparian-bank condition. Higher catch rates (i.e. CPUE) of species such as golden redhorse, northern pike *Esox lucius*, rock bass *Ambloplites rupestris*, and common shiner *Luxilus cornutus* were related to low discharge environments with high canopy cover and high percentages of basin agriculture. Downstream reaches contained high CPUE of 'large-river' species (e.g. gizzard shad, white bass *Morone chrysops*, and flathead catfish *Pylodictis olivaris*). Downstream reaches had high mean annual discharge, high proportions of shoreline rip-rap, and lower percentages of basin agriculture.

Seven environmental variables significantly explained variation in taxonomic structure using trawling data (Figure 3, lower panel). Axis 1 primarily represented a gradient of discharge, wetland land use, and substrate composition. This gradient contrasted species associated with increased discharge, increased percentage of wetland land use in local catchments, and finer substrates (e.g. freckled madtom *Noturus nocturnus*, channel catfish, and bluegill *Lepomis macrochirus*) from species associated with lower discharge and coarser substrates (e.g. hornyhead chub *Nocomis biguttatus*, slenderhead darter *Percina phoxocephala*, and northern hogsucker *Hypentelium nigricans*). Axis 2 represented a gradient of land use, which

Table III. Species distributions truncated by dams in the Iowa and Cedar Rivers, Iowa

Species common name	Iowa River	Cedar River
Shovelnose sturgeon[a]	X	
Longnose gar[a]	X	X
Shortnose gar	X	X
Bowfin[a]	X	
Goldeye[a]		X
Mooneye	X	X
Mississippi silvery minnow[a]		X
Shoal chub[a]	X	
Silver chub		X
Emerald shiner	X	X
River shiner	X	
Mimic shiner	X	
Channel shiner	X	
Blue sucker[a]	X	
Western sand darter[a]	X	
Sauger	X	X

Fish species were sampled from these rivers during 2010 and 2011. Truncated species distributions are defined as species only occurring downstream of the furthest downstream dam in each river. Species with truncated distributions are denoted with an X in each river system.
[a]Species of greatest conservation need in Iowa.

separated species associated with reaches characterized by higher percentages of basin urbanization (e.g. river shiner and bullhead minnow *Pimephales vigilax*) from species associated with reaches containing higher percentages of basin agriculture (e.g. Johnny darter *Etheostoma nigrum* and bigmouth shiner). Additionally, a pattern of increased abundance of silver chub, shoal chub, and shovelnose sturgeon in longer mainstem river fragments was identified using a three-dimensional perspective of ordination space (axes not displayed in Figure 3).

Functional trait abundance models

Tolerance guild abundance was best explained by environmental variables in the electrofishing CCA (72.2% of the total variance) compared with the trawling CCA (48.4%). Seven environmental variables were retained in the electrofishing CCA model, and three environmental variables were retained with the trawling CCA model (Figure 4, upper panels). Electrofishing CPUE of tolerant species was positively related to discharge and conductivity. The catch rate of intolerant species was positively related to coarse substrates and the percentage of basin urban land use. Electrofishing CPUE of moderately tolerant species was positively associated with the distance to upstream dams and the percentage of instream woody cover. In the trawling CCA, catch rates of tolerant species were positively related to the percentage of basin agriculture along Axis 1. Axis 2 primarily represented a gradient of substrate composition. Along Axis 2, CPUE of intolerant species related positively to the percentage of coarse

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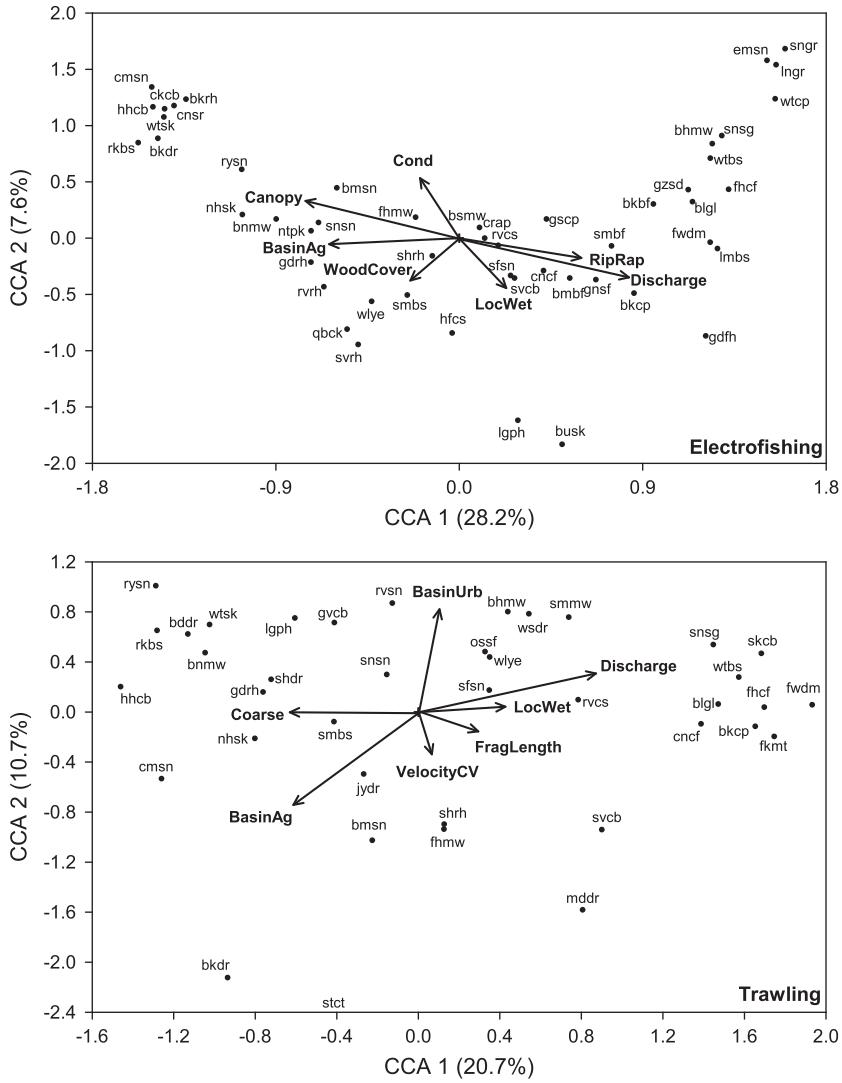

Figure 3. Canonical correspondence analyses (CCA) describing patterns of fish assemblage structure using species relative abundance (catch per unit effort) from electrofishing and trawling samples taken from 33 reaches in the Cedar and Iowa Rivers, Iowa, during 2010 and 2011. Total variance explained by axes in parentheses next to corresponding ordination axes. Habitat abbreviations are provided in Table I, and fish species abbreviations are available in Table II

substrates, whereas catch rates of moderately tolerant species were related positively to fine substrates and, to a lesser extent, flow heterogeneity (i.e. CV of velocity).

Using life history strategy data, forward selection retained six environmental variables in the electrofishing CCA (62.9% of total variation) and five in the trawling CCA (57.5%; Figure 4, middle panels). In the electrofishing CCA, Axis 1 represented a gradient of stream size, discharge, and bank alteration. Along Axis 1, catch rates of equilibrium and periodic strategists were positively related to mean annual discharge, bankfull width, and the percentage of shoreline rip-rap, whereas the CPUE of opportunistic–equilibrium strategists was negatively related to discharge and shoreline rip-rap. Additionally, catch rates of periodic and opportunistic–equilibrium strategists were positively related to mainstem fragment length. Also, electrofishing CPUE of periodic–equilibrium strategists was positively related to the percentage of basin urban land use and the percentage of woody cover. Similar to the electrofishing CCA, a discharge gradient was identified in the CCA using trawling data that had similar associations with relative abundances of periodic, equilibrium, opportunistic, and opportunistic–equilibrium strategists. The discharge gradient identified with the trawling data was slightly different, as substrate composition varied along the same gradient. Along Axis 1, CPUE of opportunistic, opportunistic–equilibrium, and periodic–equilibrium strategist was negatively related to discharge and positively related to coarse substrates, whereas catch rates of equilibrium and periodic strategists

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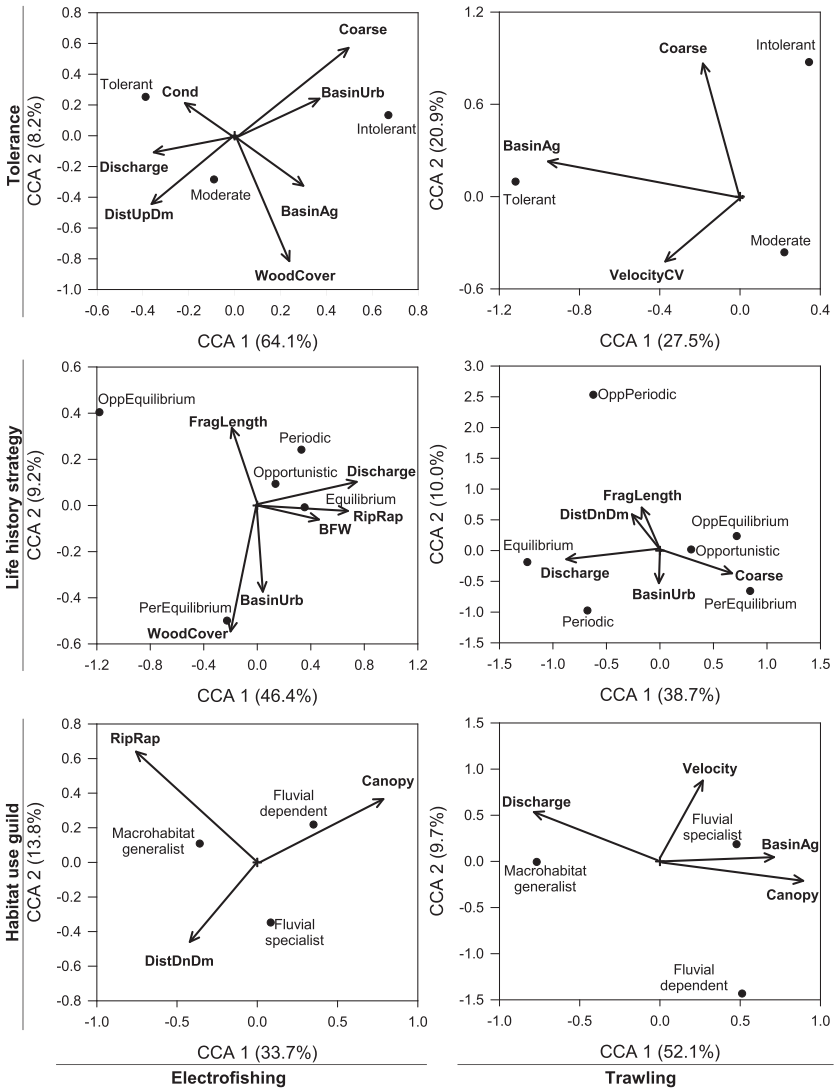

Figure 4. Canonical correspondence analyses (CCAs) describing patterns of fish assemblage structure using tolerance trait, life history strategy, and habitat use guild relative abundance (catch per unit effort) from electrofishing and trawling samples taken from 33 reaches in the Cedar and Iowa Rivers, Iowa, during 2010 and 2011. Total variance explained by axes in parentheses next to corresponding ordination axes. Habitat abbreviations are provided in Table I

were positively related to discharge and fine substrates. The trawling CCA also described CPUE of opportunistic–periodic strategists as being positively associated with distance to downstream dam and mainstem fragment length. Catch rates of periodic strategists were negatively associated with the distance to impoundments and mainstem fragment length.

Habitat use guild variation was best explained by environmental variables in the trawling CCA (61% of total variation) compared with the electrofishing CCA (47.7%; Figure 4, lower panel). Three environmental variables explained variation in CPUE of habitat guilds in the CCA using electrofishing data. Positive associations were identified between the percentage of shoreline rip-rap and CPUE of macrohabitat generalists, the percentage of canopy cover and CPUE of fluvial dependents, and distance to downstream dams and CPUE of fluvial specialist fishes. In the CCA using trawling data, four environmental variables explained variation in CPUE of habitat guilds. Axis 1 represented a gradient of discharge, basin agriculture, and canopy cover. Along Axis 1, the CPUE of macrohabitat generalists related positively to discharge; whereas CPUE of fluvial dependents and fluvial specialists was negatively related to discharge and positively related to canopy cover and basin agriculture. Additionally, Axis 2 represented a gradient of current velocity, which exhibited a positive association with the CPUE of fluvial specialists and a negative association with CPUE of fluvial dependents.

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Functional trait composition models

Five environmental variables were retained to explain 73.6% of total variation in the tolerance guild composition model (Figure 5; top panel). Along Axis 1, per cent composition of intolerant species was positively related to canopy cover and negatively related to mainstem fragment size. Conversely, per cent composition of moderately intolerant species was positively related to mainstem fragment length and negatively related to canopy cover. Along Axis 2, per cent composition of tolerant species was positively related to basin agriculture and negatively related to basin urban land use and distance to downstream impoundments.

Patterns in life history strategy composition were explained by six environmental variables (72.5% of total variation; Figure 5, middle panel). Per cent composition of opportunistic, opportunistic–equilibrium, and periodic–equilibrium strategists was positively related to coarse substrate and negatively related to discharge. On the other hand, per cent composition of periodic and equilibrium strategists was positively related to discharge. Also, per cent composition of opportunistic–periodic strategists was positively associated with mainstem river fragment length. Along Axis 2, river reaches with high discharge, high proportions of upstream urban land use, and low proportions of woody cover were associated with a high

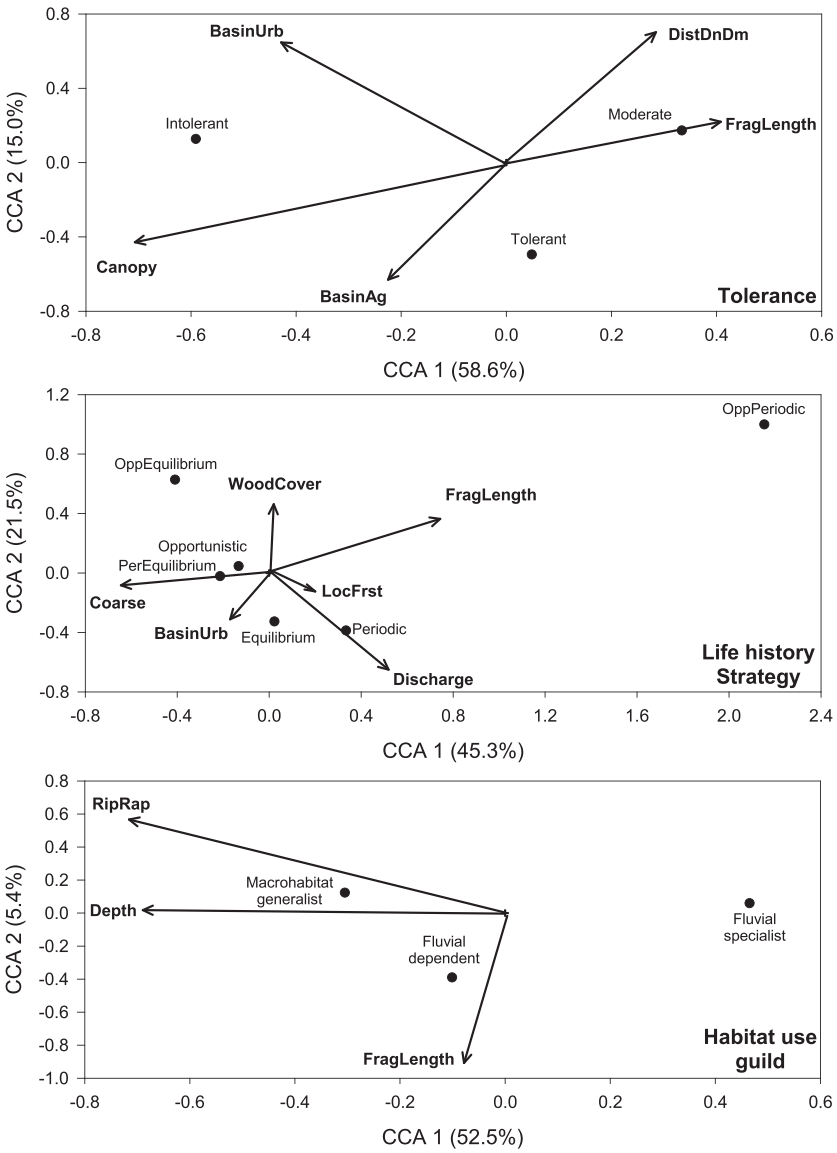

Figure 5. Canonical correspondence analyses (CCAs) describing patterns of fish assemblage structure described through per cent composition of tolerance trait, life history strategy, and habitat use guild from species composition described using both electrofishing and trawling samples taken from 33 reaches in the Cedar and Iowa Rivers, Iowa, during 2010 and 2011. Total variance explained by axes in parentheses next to corresponding ordination axes. Habitat abbreviations are provided in Table I

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per cent composition of equilibrium strategist and a low composition of opportunist–equilibrium strategists.

The habitat use guild composition model retained three environmental variables using forward selection (57.9% of total variation; Figure 5, lower panel). Axis 1 represented a gradient of depth and rip-rap. Along Axis 1, per cent composition of macrohabitat generalists was positively related to mean depth and the percentage of shoreline rip-rap. Conversely, per cent composition of fluvial specialists was negatively related to mean depth and the percentage of shoreline rip-rap. Along Axis 2, per cent composition of fluvial-dependent species was positively related to mainstem river fragment length.

Partitioning model variance

Results from the pCCAs indicated that reach-scale environmental variables were generally more important in explaining fish assemblage structure than landscape-scale and dam-related environmental variables (Figure 6). Reach-scale environmental variables accounted for 25.0–81.1% of constrained fish assemblage variation in almost all of the CCA models. Among reach-scale variables, mean annual discharge was commonly selected in the CCAs and explained the most assemblage variation compared with other reach-scale characteristics. Among other reach-scale variables, the percentage of shoreline rip-rap also explained high proportions of fish assemblage variation when selected. The variation not explained by reach-scale characteristics was largely explained by dam and (or) land use variables. Altogether, land use variables explained 5.8–47.2% of the assemblage variation in nine CCA models and were largely represented by either the percentage of basin agriculture and (or) urban land use. Variables associated with dams were identified in nine CCA models and explained 6.2–25.1% of the variation in fish assemblages (mainly represented by fragment length and distance to impoundment). Land use variables explained more of the assemblage variation than variables associated with dams in six CCA models, particularly in the tolerance guild CCAs and the CCAs using trawling data. In contrast, variables associated with dams accounted for as much or more of the variation in life history strategies as landscape-scale variables.

DISCUSSION

Fish assemblage structure in the Cedar and Iowa Rivers was influenced by a variety of environmental characteristics operating at multiple spatial scales. From a geographic perspective,

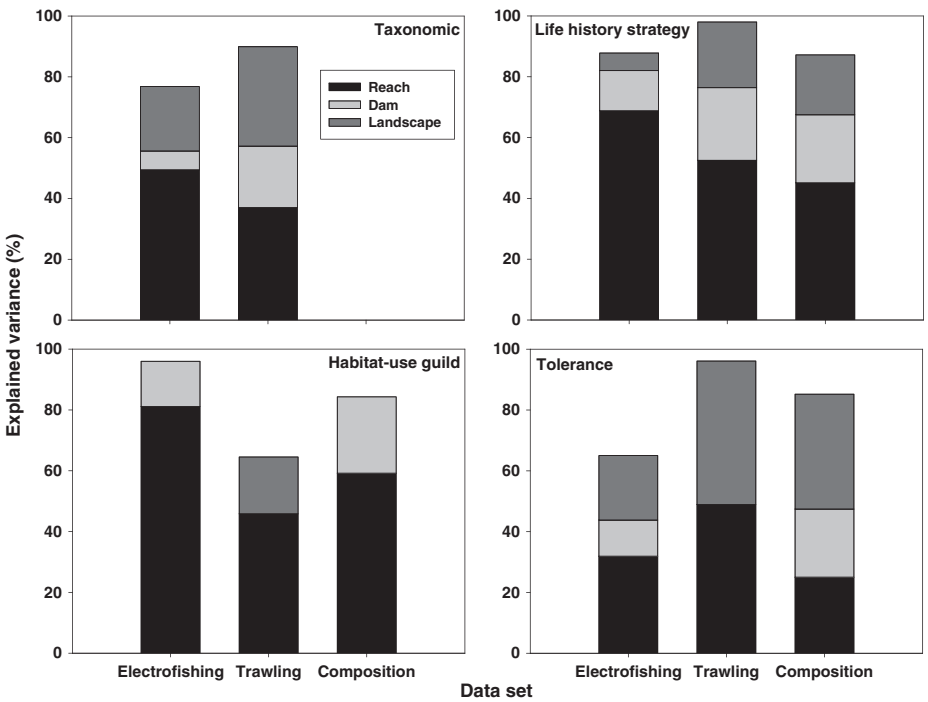

Figure 6. Percentages of explained variance in fish assemblage structure described in 11 canonical correspondence analysis models. Total constrained variance in fish assemblages was partitioned by reach-scale, dam-related, and landscape-scale environmental variable sets. Fish assemblages were described by taxonomic abundance, trait abundance, and trait composition using electrofishing and trawling datasets. Fish trait classifications included tolerance guilds, life history strategies, and habitat use guilds. Fish assemblage structure was described using data acquired from electrofishing and trawling samples taken from 33 reaches in the Cedar and Iowa Rivers, Iowa, during 2010 and 2011

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spatial patterns of species occurrence and trait composition were longitudinal in structure and were largely explained by mean annual discharge and other reach-scale habitat variables. Although longitudinal variation in fish assemblage structure was associated with reach-scale habitat, other ecological patterns of functional trait abundance and composition were attributed to environmental variation associated with dams and watershed land use. These results provide further evidence suggesting that lotic fish assemblages are structured by cumulative environmental influences of natural and anthropogenic origin, exhibited across multiple spatial scales (Weigel *et al*., 2006; Hoeinghaus *et al*., 2007; Rowe *et al*., 2009; Wang *et al*., 2011; Sindt *et al*., 2012).

Agricultural land use, particularly row-crop agriculture, dominates much of the landscape in the state of Iowa. Because of this land use saturation, percentages of basin agriculture exhibited little variation among sampling reaches compared with reach-scale characteristics such as discharge. Hence, fish assemblage structure was primarily influenced by reach-scale characteristics as opposed to landscape measures in the Cedar and Iowa rivers. Multi-scale analyses in other systems have typically described the overarching importance of landscape characteristics on habitats and species distributions (Marsh-Matthews and Matthews, 2000; Hoeinghaus *et al*., 2007). Our results differed in that taxonomic structure was largely influenced by local environmental characteristics. Rather, our results are concordant with those of Rowe *et al*. (2009) and Fischer and Paukert (2008) where the explanatory power of local-scale environmental characteristics exceeded the large-scale influences on fish assemblage structure in relatively homogenous (i.e. agriculturally dominated) landscapes.

Despite the relative importance of reach-scale habitat, our models indicated that land use variables were still important determinants of fish assemblages in the Iowa and Cedar Rivers. In particular, land use characteristics explained high proportions of tolerant guild variation. For instance, the trawling abundance and per cent composition of tolerance fish species exhibited positive relationships with agricultural land use. Similar studies have found that lotic systems with upstream agricultural land use exceeding 50% of the watershed have been associated with lower scores of fish biological integrity (Wang *et al*., 1997) and higher proportions of tolerant species (Rowe *et al*., 2009). Surprisingly, CCA models contained very few land use factors measured in local catchments, despite high variation in the variables. Additionally, we did not anticipate the positive association between basin urban land use and intolerant species in the electrofishing model and functional trait composition model. Urban land use exceeding 10–15% of the watershed is often considered a threshold where declines in biological integrity tend to occur (Wang *et al*., 1997). Most of our reaches did not exceed 9% urban land use. Nonetheless, the influence of landscape factors was minor compared with the influence of reach-scale habitat on the organization of fish assemblages in our study systems.

Among reach-scale characteristics, longitudinal changes in discharge provided the strongest explanation for spatial changes in the local fish assemblage structure in the Iowa and Cedar Rivers. The relative importance of mean annual discharge and its inclusion in the majority of CCA models likely indicates that fish assemblage structure was highly influenced by the flow regime. In general, it is assumed that discharge characterizes broad habitat types that correspond to patterns in species composition along the length of a river (i.e. zonation; McGarvey and Ward, 2008; McGarvey, 2011). Unlike the longitudinal patterns of species richness often exhibited in lotic systems in the western USA (e.g. Rahel and Hubert, 1991), longitudinal patterns in lowland rivers of the Midwest reflect gradual downstream changes in fish species distributions (McGarvey, 2011; Sindt *et al*., 2012; Pierce *et al*., 2013) and assemblage function (Vannote *et al*., 1980; Junk *et al*., 1989). Longitudinal shifts in fish assemblages are typically linked to changes in river position or river size, yet assemblage structure should ultimately be controlled by streamflow. Discharge provides both habitat volume and complexity (Poff *et al*., 1997) and can be altered by various anthropogenic activities (Ward and Stanford, 1995). Recent work by McGarvey (2011) demonstrated how gradual downstream shifts (i.e. every 50 rkm) in discharge are inherently linked to longitudinal zonation patterns of fish assemblages. Zonation patterns tend to be the result of a broad habitat type characterized among adjacent river reaches (Matthews, 1998). Our findings agree with those of McGarvey (2011) and suggest that spatial changes in species composition (i.e. replacements) in the Cedar and Iowa Rivers correspond to downstream transitions in discharge and broad habitat types (e.g. upstream reaches similarly characterized by lower discharge, increased canopy, and coarse substrates).

Our observations on flow variability, described by annual discharge CV values, provide additional insight on the spatial association between mean annual discharge and fish assemblages in the Cedar and Iowa Rivers. Specifically, spatial patterns of inter-annual flow variability may provide a habitat template that links fish life history strategies and mean annual discharge in the Cedar and Iowa Rivers. Although the annual discharge CV values were not included in the ordination analyses, annual discharge CV exhibited a strong negative correlation with mean annual discharge, thereby suggesting a spatial link between fish assemblage temporal flow variation. Specifically, increased discharge and low variability in downstream habitats were associated with increased abundance and per cent composition of equilibrium strategists, whereas low discharge and high variability in upstream river habitats corresponded to increased abundance and per cent composition of opportunistic–equilibrium and opportunistic strategists.

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Life history correspondence to spatial changes in flow variability suggests that there is an environmental stability gradient along the Cedar and Iowa Rivers. Links between flow variation and life history patterns have often been described by this habitat template (Poff, 1997), especially among upstream and downstream habitats (Schlosser, 1990; Roberts and Hitt, 2010; Pease *et al*., 2012). Small-bodied opportunistic species are capable of colonizing and reproducing in variable lotic environments (e.g. riffles and flashy streams) characterized by low streamflow (Schlosser, 1990; Winemiller and Rose, 1992; Hitt and Roberts, 2012). The short life span and fast maturation of opportunistic species allow for a fast recovery and re-colonization in more variable lotic environments that are more prone to flashy disturbance (Schlosser, 1990). Small-bodied opportunists also increase their persistence by using variable environments to avoid predation from larger-bodied species common in stable environments (Hoeinghaus *et al*., 2007; Pease *et al*., 2012). In downstream river habitats, equilibrium species tend to persist in environments with higher discharge, which typically reflect higher levels of environmental stability (i.e. less flashy and more predictable flow regimes). High discharge habitats, in conjunction with adequate amounts of instream structure, provide an environment capable of supporting the reproductive ecology of large-bodied equilibrium strategists (Winemiller and Rose, 1992; Mimms and Olden, 2012; Pease *et al*., 2012).

Apart from the influence of discharge, rip-rap characteristics were also consistently identified as an important reach-scale habitat component in the Cedar and Iowa Rivers. Rip-rapped shorelines (e.g. rocks and tires) have been associated with poor biological integrity, alteration of channel morphology, and loss of ecosystem function (Lyons, 2005). However, shoreline rip-rap has been shown to increase habitat complexity and fish diversity in large rivers (White *et al*., 2009; Eitzmann and Paukert, 2010) and have characterized unique patterns in species composition compared with other habitats along channel borders (Madejczyk *et al*., 1998). Recently, White *et al*. (2009) found that engineered habitats in the Kansas River composed of rip-rapped shoreline had a positive influence on the diversity and abundance of macrohabitat-generalist and fluvial-dependent fish species. This observation is different from fish assemblage patterns observed in the Cedar and Iowa Rivers, where rip-rap was positively related to the abundance and richness of macrohabitat generalists and negatively related to the abundance and richness of fluvial specialists. Compared with habitat described by Eitzmann and Paukert (2010), the Iowa and Cedar Rivers seem to exhibit higher habitat heterogeneity than the Kansas River. It may be likely that rip-rap does not provide the same benefits in the Cedar and Iowa Rivers as observed in the Kansas River. The lack of fluvial specialists in reaches with high proportions of rip-rap further supports the notion that this form of artificial habitat is not typically used by fluvial specialists in our study systems. Rip-rap revetments were apparent in all study reaches, which implies that our analysis probably showed a measurable association with fish assemblages. However, the effects of rip-rap were probably intensified near sites of multiple disturbances (e.g. reaches below dams or in urbanized flood plains). Our results and the results of Lyons (2005) indicate that further investigation is needed to understand the influence of rip-rap on fish assemblages in lotic systems throughout the upper Mississippi River drainage.

Previous work by Rowe *et al*. (2009) and Neebling and Quist (2010) demonstrated how landscape disturbance and habitat were associated with fish assemblages in lotic systems in Iowa but did not evaluate dams. Pierce *et al*. (2013) documented a strong pattern of fish assemblage change associated with presence of dams along three eastern Iowa rivers, but the pattern was confounded with longitudinal position. They also found similar truncated patterns of species distributions with many species that were limited to the furthest downstream reaches. Because numerous environmental factors (e.g. discharge) influenced fish assemblages, dams were expected to account for only a fraction of the variance in fish assemblage structure. Studies similar to ours have observed small to moderate (6–19%) percentages of fish assemblage variation explained by dams (Weigel *et al*., 2006; Wang *et al*., 2011). For instance, comparing with local-scale and basin-scale environmental factors in Wisconsin's nonwadeable rivers, Weigel *et al*. (2006) found that only small amounts of fish assemblage variation could be explained by dams when using metrics from the index of biotic integrity (IBI). Similarly, Wang *et al*. (2011) studied unimpounded reaches of streams and rivers in Wisconsin and Michigan and found that dams also accounted for small amounts of variation in IBI metrics and other fish traits. Compared with these studies, our study found that variables associated with dams accounted for a larger percentage of fish assemblage variation in both functional trait and taxonomic descriptors. Again, this was probably due to the homogeneous landscape in Iowa where local habitat and dams may play a larger role in structuring fish assemblages. Nonetheless, our study was most similar to that of Weigel *et al*. (2006) because both studies assessed only nonwadeable rivers and used the same variables associated with dams. Much like the work of Weigel *et al*. (2006), Wang *et al*. (2011), and Pierce *et al*. (2013), our research suggests that dams play a considerable role in influencing the taxonomic and functional organization of fish assemblages in nonwadeable rivers.

Two prominent relationships between dams and fish assemblages were identified among other environmental relationships. Mainstem fragment length played a considerable role in influencing the relative abundance of opportunist–periodic strategists (e.g. silver chub and shoal chub). Perkin and Gido (2011) described similar findings when they determined a minimum size threshold of river fragments that was

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needed for the persistence of pelagic-spawning cyprinids (i.e. silver chub and shoal chub) in rivers of the Great Plains. Similarly, Pool *et al*. (2010) found that small fragments between dams created unfavourable hydrologic conditions for species with opportunistic–periodic strategies. When in close proximity to impounded habitats or in impounded small river fragments, we observed high abundance of periodic strategists. Falke and Gido (2006) described a similar pattern in Kansas rivers where highly abundant facultative reservoir species exhibiting periodic strategies (e.g. gizzard shad, walleye, and buffalo species *Ictiobus* spp.) were located in close proximity to impoundments. Additionally, our observations of fish assemblages in close proximity to impoundments were characterized by high percentages of tolerant species and low percentages of moderately tolerant species. This finding may indicate that spatial effects from impoundments partially dictate patterns of biological integrity (Santucci *et al*., 2005; Wang *et al*., 2011).

Beyond the influence of mainstem fragment length, it is evident that dams have limited the longitudinal distribution of several fish species. Similar to the findings of Pierce *et al*. (2013), the distribution of fish species in the Iowa and Cedar Rivers exhibited longitudinal variation, yet many 'downstream distributed' fish species appeared to be limited by dams. Of the 15 species with truncated distributions in our study, nine species also had truncated distributions in three other Iowa rivers (Pierce *et al*., 2013). Historical records of fish distributions confirmed that species such as mooneye, shortnose gar, and emerald shiner were widely distributed in both the Iowa and Cedar Rivers (Loan-Wilsey *et al*., 2005; Parks *et al*., 2014), implying that the farthest downstream dams limit the longitudinal dispersal of fishes. Similar patterns of truncated species distributions were observed by Santucci *et al*. (2005) where dams created barriers to fish dispersal in an Illinois river system. In our study, most of the species that were limited by dams typically occur in 'great rivers' (e.g. Mississippi River) and exhibit complex migratory behaviours (Galat and Zweimuller, 2001). Many of these fish species are known to make considerable longitudinal movements along the main channel as well as lateral migrations to floodplain environments to access critical habitats to complete important life history events (Junk *et al*., 1989; Galat and Zweimuller, 2001). The construction of dams has probably restricted the movements of many 'downstream distributed' river species and resulted in the isolation and extirpation of several large-river fishes upstream of dams in the Iowa and Cedar Rivers. For instance, species such as longnose gar and mooneye have not been observed in habitats upstream of the Cedar Rapids Milldam since 1891 (Loan-Wilsey *et al*., 2005).

Our study provides valuable insights about the roles of land use, dams, and reach-scale environmental characteristics on fish assemblages in nonwadeable rivers in Iowa. This is the most comprehensive evaluation of how fish assemblages are related to dams in Iowa's nonwadeable rivers. The addition of trawling data has greatly improved our understanding of how benthic fish assemblages respond to riverine environments, and the use of several fish assemblage descriptors such as taxonomy, life history strategies, tolerance traits, and habitat use guilds has enabled us to connect ecological and distributional patterns with environmental variation. These diagnostic considerations are especially important when trying to determine the appropriate metrics used to assess disturbance or to evaluate the success of restoration and mitigation efforts in river ecosystems.

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