Fish assemblages in Iowa's nonwadeable rivers: historic changes in assemblage structure and relationships with natural and anthropogenic environmental characteristics

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Fish assemblages in Iowa’s nonwadeable rivers: historic changes in assemblage structure and relationships with natural and anthropogenic environmental characteristics

by

Timothy Patrick Parks

A thesis submitted to the graduate faculty in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Fisheries Biology

Program of Study Committee:

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Iowa State University
Ames, Iowa
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Finally, I want to thank my family for their support. I would like to dedicate this thesis to my late mother, Catherine Parks, who encouraged me to share my creative talents in science and music with others. Without her laughter, goofiness, and inspiration, I would not be the person I am today.
CHAPTER 1. GENERAL INTRODUCTION

Nonwadeable or large rivers are dynamic aquatic ecosystems capable supporting high fish biodiversity (Allan and Flecker 1993). Due to human exploitation of lotic systems and landscapes, river and stream ecosystems have become highly imperiled (Allan and Flecker 1993; Dudgeon et al. 2006) along with their associated fish assemblages (Jelks et al. 2008; Burkhead 2012). Large river ecosystems are particularly influenced water development activities (i.e., dam construction; Ward and Stanford 1995; Poff et al. 1997) and from cumulative impacts from upstream land use (Allan 2004). Although much work has gone into studying ecology of rivers, there is still an incomplete understanding of how riverine fish assemblages respond to anthropogenic disturbances.

Many river systems throughout the midwestern U.S. have been highly degraded due to human activities (Karr et al. 1985; Gido et al. 2010). Natural environments were largely transformed for agricultural practices, urban land use, and water development, throughout the Midwest, particularly in Iowa. Over the last 150 years, approximately 78% of Iowa’s original landscape (e.g., grassland, wetland, and forests) was transformed by row crop agriculture (Gallant et al. 2011). During the early history of landscape transformation in Iowa, many wetlands and riparian floodplains were drained and rivers were channelized resulting in permanent damage to Iowa’s lotic ecosystems (Menzel 1983). Riverine ecosystems have been also altered through dam construction, in which 246 structures currently fragments major rivers in Iowa (Hoogeveen 2010). Compared to other lotic disturbances, dams have been characterized as the primary driver of altered stream flow in the U.S. (Carlisle et al. 2011). Humans have also contributed to the widespread introduction
and establishment of non-native fishes which have can have many negative consequences on ecosystem function (Bernstein and Olson 2001). Altogether, these human activities are largely responsible for the changes that have occurred throughout terrestrial and lotic ecosystems in Iowa (Menzel 1983; Zohrer 2006).

The events associated with anthropogenic disturbance in Iowa’s river ecosystems have been linked to the concurrent extirpation and decline of numerous fish species (Menzel 1981, 1987). Many explanations for species declines remain valid, yet the recent detections of supposedly extirpated species (e.g., western sand darter *Amocrypta clara*; Neebling and Quist 2008) and the unknown ecology of many riverine fish species has catalyzed the need to re-evaluate the status of fish assemblages in Iowa’s nonwadeable rivers. A better understanding of spatiotemporal dynamics in species distributions can help to improve and reprioritize conservation efforts that are currently allocated to the 68 fish species listed as species of greatest conservation need in Iowa (Zohrer 2006). In addition to increased conservation efforts, the knowledge of spatiotemporal changes in fish assemblage structure associated with anthropogenic disturbance may be insightful when considering efforts to create or recalibrate measurements of ecological integrity in rivers (Schlosser 1990; Buegley and Pyron 2010).

In response to these conservation and management needs, the objectives of this thesis were to 1) evaluate the historic changes in fish assemblages that occurred in Iowa’s interior nonwadeable rivers via representative changes occurring in five focal river systems and 2) determine the relationship between fish assemblage structure and environmental characteristics measured at multiple spatial-scales. It was anticipated that both objectives
would provide added insight on how anthropogenic factors influence the organization of riverine fish assemblages.

**Thesis Organization**

The following chapters in this thesis consist of two research chapters and a general conclusion chapter. The research chapters are written in styles specific to the scientific journals where they will be submitted for publication. The first research chapter (i.e., Chapter 2) is a manuscript that will be submitted to the *American Midland Naturalist* and the second research chapter (i.e., Chapter 3) will be submitted to *River Research and Applications*.

**References**


CHAPTER 2. HISTORIC CHANGES IN FISH ASSEMBLAGE STRUCTURE IN MIDWESTERN NONWADEABLE RIVERS

A manuscript to be submitted for publication in the *American Midland Naturalist*.

Timothy P. Parks\(^1,2\), Michael C. Quist\(^3\), Clay L. Pierce\(^4\)

**ABSTRACT**

Historic change in fish assemblage structure was evaluated in the mainstems of the Des Moines, Iowa, Cedar, Wapsipinicon, and Maquoketa rivers, in Iowa. Fish occurrence data were compared in each river between historic and recent time periods to characterize temporal changes among 126 species distributions and assess spatiotemporal patterns in faunal similarity. A resampling procedure was used to estimate species occurrences in rivers during each assessment period and changes in species occurrence were summarized. Shifts in species composition were analyzed at the river and river section scale using cluster analysis, species turnover, and analysis of multivariate beta dispersion. The majority of species exhibited either increases or declines in distribution in all rivers with the exception of several “unknown” or inconclusive trends exhibited by species in the Maquoketa River. Cluster analysis identified temporal patterns of similarity among fish assemblages in the Des

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Moines, Cedar, and Iowa rivers within the historical (AU = 0.92) and recent (AU = 0.95) assessment period indicating a significant change in species composition. Prominent declines of backwater species with phytophilic spawning strategies contributed to assemblage changes occurring across river systems.

**INTRODUCTION**

Increased anthropogenic alteration of lotic systems and the decline of many fishes have prompted a growing concern for native fish conservation in North America (Abell *et al.*, 2002; Jelks *et al.*, 2002). The successful conservation of lotic fish fauna is dependent upon an adequate understanding how fish faunas change through time and space (Matthews, 1998; Jackson *et al.*, 2001). In the last 10 years, large river ecosystems and fish assemblages have been a major conservation focus, largely due to our limited understanding of their response to anthropogenic impacts (Johnson *et al.*, 1995). Large rivers provide highly diverse habitats that are capable of supporting the life history of many different fishes (Sparks, 1995; Poff *et al.*, 1997). Over the past 150 years, large rivers have been increasingly subjected to the cumulative effects of anthropogenic disturbances such as pollution, urbanization, agriculture, channel modification, and impoundment (Sparks, 1995; Hughes *et al.*, 2005). These human disturbances have directly and indirectly influenced fish assemblage structure by altering flow regimes (Poff *et al.*, 1997), degrading water quality and habitat structure, disrupting energy inputs, shifting biotic interactions (Karr *et al.*, 1986), and fragmenting river corridors (Dynesius and Nilsson, 1994). The effects of disturbance can be observed through temporal declines of specialist fishes and the subsequent expansion of generalist fish species (Karr *et al.*...
al., 1885; Scott and Helfman, 2001). As shifts in fish assemblages occur more frequently across river systems, overall patterns of beta diversity indicate that fish assemblages tend to become increasingly homogeneous across large geographic areas (Olden and Rooney, 2006; Rahel, 2010). Homogenized faunal states are hard to reverse and may lead to future conservation failures (Rahel, 2010). Therefore, successful conservation actions depend on adequate long-term spatiotemporal studies of river fish assemblages to understand mechanisms responsible for shifts in assemblage structure (Matthews, 1998; Jackson et al., 2001; Hughes et al., 2005).

Like many other Midwestern rivers, Iowa’s rivers contain diverse fish faunas, yet there is an incomplete understanding about the distribution and ecology of these fishes. In Iowa, 44% (i.e., 68 species) of all animal species listed as species of greatest conservation need (SGCN) are fish (Zohrer, 2006). Since large river tributaries of the upper Mississippi River basin (UMRB) are known to contain high fish biodiversity (Burr and Page, 1986; Neebling and Quist, 2010; Pierce et al., In press), the majority of the 68 fish SGCN are primarily distributed in Iowa’s large nonwadeable rivers. Previous studies have been conducted to assess the distributions of fishes in Iowa’s nonwadeable rivers (Gelwicks and Simmons, 2007; Neebling and Quist, 2010), but only a few studies have been conducted to determine the historic status of stream and river fishes in the state (Menzel, 1981, 1987; Palić et al., 2007; Sindt et al., 2011). Typically, status evaluations compare historical and contemporary fish occurrence data to evaluate temporal trends (Patton et al., 1997; Gido et al., 2010). Once historic dynamics of fish distributions are determined, inference can be made about the limitations of species including the degradation, loss, or fragmentation of critical habitats (Karr et al., 1985; Angermeier, 1995).
Interior rivers of Iowa have long histories of anthropogenic disturbance which has been linked to the impairment of lotic fish faunas at local and regional scales (Menzel, 1981; Poff and Allan, 1995). Gallant et al., (2011) estimated that 85% of Iowa’s natural landscape has been converted to an agriculturally-based landscape. Along with Iowa’s transformed landscape, 246 mainstem dams currently fragment large rivers (Hoogeveen, 2010). Water development activities and land use in the watershed have been shown to alter the natural flow regime which can have a considerable influence on the biophysical factors controlling lotic ecosystems (Menzel, 1983; Poff et al., 1997; Bunn and Arthington, 2002). Flow disturbance has been shown to increase annual discharge in large, Iowa rivers over the last 60 years due to changes in land use and precipitation (Schilling and Libra, 2003). In addition to hydrologic alterations, anthropogenic disturbances can also fragment habitats. In particular, dams fragment river corridors and act as dispersal barriers that truncate fish distributions (Santucci et al., 2005; Catalano et al., 2007) and isolate and contribute to the extirpation of fishes upstream of dams (Sheldon, 1987; Quist et al., 2005). Other than physical changes to lotic habitat, the introduction of non-digenous species from various stocking practices have also lead to negative consequences for native ichthyofauna in Iowa (Bernstein and Olson, 2001).

The purpose of this study was to investigate changes in the historic ichthyofauna of five nonwadeable rivers in Iowa. This was accomplished by evaluating long-term trends of species’ spatial distributions. We also assessed and compared historic and recent species composition in each river to describe spatiotemporal patterns of faunal similarity and determine whether assemblages have become homogenized. We expected obvious temporal differences in taxonomic composition across rivers. We specifically hypothesized that
changes in species composition described through the number of species declines would vary among rivers, due to the unequal magnitude of anthropogenic disturbance across the landscape and rivers. We also expected to observe strong temporal differences in faunal similarity across rivers. Based on knowledge of widespread habitat degradation and the introduction of non-indigenous species (e.g., stocking practices), we expected fish faunas to become more taxonomically similar over time.

METHODS

STUDY AREA

Historic ichthyofaunal changes were assessed in the mainstems of the Des Moines, Iowa, Cedar, Wapsipinicon, and Maquoketa rivers (Fig. 1; upper panel). These river drainages form the majority of the UMRB in Iowa and were chosen because they represent high levels of fish biodiversity. The rivers flow northwest to southeast and drain areas varying from 4,808 to 37,141 km² (Table 1). Average precipitation varies 87.5–90.3 cm among basins (Falcone et al., 2010). Although the surficial geology varies within and among river basins, soil texture is similar and includes coarse sandy-loams in the upstream reaches to fine silty-loams in the downstream reaches of each river [National Hydrography Dataset (NHD); U.S. Geological Survey; I.S.U., 2004].

Numerous landscape and instream alterations have occurred in our study rivers over the past 150 years; however, the majority of these changes could only be quantified since the 1950s (Table 1; Falcone et al., 2010). During Iowa’s initial settlement in the 1850s, the landscape was composed of about 69% prairie, 19% forest, and 12% wetlands (Zohrer, 2006;
Gallant et al., 2011). In contrast, recent land cover consists of 75-80% agriculture (i.e., row crop and pasture) and 6-9% urban land cover among basins (Table 1; Falcone et al., 2010). Agriculture and urban land cover compose 20-45% and 7-11% of mainstem riparian areas, respectively. The number of major dams [i.e., dam height > 15 m or dam storage > 6,150 mega liters (ML) per km²] and mainstem low-head dams varies from 7-10 in each mainstem river. Since 1950, the per-basin water storage (i.e., impoundments) increased from 0.8-94.5 ML/km² across river basins. Since 1970, the number of dams per basin constructed increased from 4-459 (i.e., mainstem and tributaries). Across study rivers, 19-65% total river length has been altered by dams and impoundments, channel modification, and other instream development.

DATA ACQUISITION

Fish data from 1884 to 2011 were gathered from a variety of sources and databases. Historic and recent data were acquired from the Iowa GAP (IAGAP) database (Loan-Wilsey et al., 2005), which is the most comprehensive source of historical fish species distribution data for Iowa’s streams and rivers. Additional fish occurrence data were acquired from Wilton (2004), Gelwicks (2006), Neebling and Quist (2010), and additional sampling completed by the authors during the summers of 2010 and 2011. As data were compiled for the IAGAP database, an extensive literature review was conducted to screen and cross-reference the validity of historical fish distributions (Loan-Wilsey et al., 2005). Fish distribution data were entered into a database and georeferenced to mainstem river segments and to eight-digit hydrologic unit basins (HUC-8 basins) defined by the NHD using a geographic information system (Arc GIS 9.3, Environmental Research Institute, Redlands,
Only mainstem, nonwadeable river samples were considered for our analyses; no major tributaries were included. Our analysis was limited to using species presence-absence data to reduce uncertainty associated with variable times of sampling (i.e., time of year), variable or unknown sampling effort, and the use of different sampling gears (e.g., seines, trawls, and electrofishing).

**DATA ANALYSIS**

Historic changes in fish distributions were described by comparing species occurrences from historic and recent assessment periods. To determine the time span of each assessment period, fish survey samples were pooled over time in each river until an adequate spatial distribution (i.e., longitudinal distribution) of samples was achieved. We defined an adequate spatial distribution of samples as a minimum of four mainstem sampling events per HUC-8 basin. The duration of each assessment period was also determined using historical events likely linked to changes in fish assemblage structure (e.g., increases in agricultural practices). We defined the historic time period as 1884-1969 (Fig. 1; lower, left panel). This time period includes the earliest historical sampling efforts (Jordan and Meek, 1884), the first comprehensive statewide fish survey effort that coincided with the advent of electrofishing in the 1950s, and the time period before a major statewide increase in row crop agriculture in the 1970s. Additionally, 1970 is considered a standard threshold by the U.S. Environmental Protection Agency when assessing historic fish distributions to calculate faunal intactness (USEPA, 2009). We defined the recent sampling period as 1990-2011 (Fig. 1; lower, right panel). This time period reflected an era of increased gear efficiency and also represented a period of time when expansion of agricultural land use stabilized across Iowa (Zohrer, 2006,
Gallant et al., 2011). Due to the influx of landscape and instream disturbances during 1970-1989, environmental legislative transitions, and a desire to provide a “buffer” between historic and recent assessment periods, we excluded data from 1970-1989.

Species distributions were quantified using percent occurrence in each river for both assessment periods. Percent occurrence described the proportion of the total number of NHD river segments where a species was present in each river. Since sampling effort was unevenly distributed among rivers, a randomized sampling procedure was used to estimate percent occurrence for each species. Similar to Gido et al., (2010), a random subset of fish sample \( n \) locations was iteratively sampled in each river to estimate species occurrences. Resampling was performed 1,000 times for every species in each river and assessment period. To determine trends, iterations (i.e., percent occurrence value) from the recent assessment period were subtracted from corresponding iterations from the historic period to create a distribution of differences. Differences in percent occurrence iterations were calculated between assessment period iterations (i.e., 1,000 differences) and were used to calculate 95% confidence intervals needed for trend determination (Johnson, 1999). If a confidence interval included zero, then a species distribution exhibited no historic change. Conversely, if confidence intervals exhibited only positive differences or negative differences, then a species has either declined or an increased in distribution, respectively. Unknown trends in species distributions were defined as those in which a species was detected less than three times in historic samples. Only non-native species introductions were exempt from this unknown trend determination.

Historic trends were summarized for each river as the percentage of species exhibiting increases, declines, no changes, or unknown trends. Trends were also summarized
for fish species of greatest conservation need (SGCN). Additionally, we assessed the faunal structure of increasing and declining trends using family membership and trophic, reproductive, and habitat traits. We used pre-defined trait classifications of fish reproductive guilds (Balon, 1978), trophic guilds (Becker, 1983; Lyons, 1992; Poff and Allan, 1995; Goldstein and Meador, 2005) and family membership (Pflieger, 1997). Habitat traits from multiple sources (Kinsolving and Bain, 1993; Lyons et al., 2001; Schramm, 2004; Goldstein and Meador, 2005; Falke and Gido, 2006; Geutreuter et al., 2010) were used to classify fish into habitat-use guilds. Habitat generalists were classified as fishes that could complete their life history in a variety of habitats including altered habitats. Habitat generalists were species that could be considered facultative reservoir species (Falke and Gido, 2006) or macrohabitat generalists (Kinsolving and Bain, 1993). Backwater species were classified as fishes with specialized life histories that rely on non-degraded off-channel habitats (Schramm, 2004; Goldstein and Meador, 2005; Geutreuter et al., 2010). Fluvial species were classified as those with life histories dependent on fluvial habitats (Kinsolving and Bain, 1993; Lyons et al., 2001).

Historic patterns in faunal similarity were assessed using species composition data measured at the river and river section scale. The river scale was defined as the entire mainstem river; whereas the river section scale was defined by mainstem river partitions delineated by the perimeters of HUC-8 basins (Armitage and Rankin, 2009). Jaccard’s distance matrices were created using historic and recent species composition data assessed at both spatial scales. Distance matrices were analyzed with cluster analysis to describe spatiotemporal shifts in faunal composition. Hierarchical cluster analysis was used to assess patterns in faunal similarities among rivers using an overall distance matrix from both
assessment periods and separate distance matrices from each assessment period (Hansen and Ramm, 1994; Hoagstrom et al., 2007; Gido et al., 2010). Ward’s minimum variance linkage was chosen to construct cluster dendrograms. Ward’s linkage is able to retrieve clusters from a variety of data structures and has been shown to consistently provide better classifications than most agglomerative linkages when data overlap in multivariate space (Milligan and Cooper, 1987; Hansen and Ramm, 1994). To aide in the interpretation of clusters within dendrograms, we evaluated cluster significance with a post hoc bootstrap resampling procedure. Bootstrapped cluster evaluation, described by Suzuki and Shimodira (2009), provides alternative unbiased (AU) index values that determine statistically meaningful clusters and allow for improved ecological interpretation (Jackson et al., 2010). High AU values indicate meaningful clusters that show consistent groupings from re-sampled observations; therefore, we determined cluster significance criteria at AU values $\geq 0.90$ (Singh et al., 2011). Clusters of river observations were interpreted by comparing shared, distinct species occurrences. Cluster analyses and bootstrap cluster evaluation were performed using the pvclust package in R (R Development Core Team, 2011).

In addition to cluster analysis, temporal species turnover was also evaluated in each river and HUC-8 river section using dissimilarity values obtained from the Jaccard’s distance matrices (i.e., turnover defined as 1-Jaccard’s similarity; Legendre and Legendre, 1998). Matching observations (e.g., historic versus recent Cedar River) were used to select dissimilarity values from the distance matrix. Turnover values were plotted for each river and HUC-8 river section to compare the magnitude of temporal change in species composition. Similar to the analysis used by Roberts and Hitt (2010), HUC-8 percent
dissimilarities were used to identify where species turnover was occurring and gauge the contribution of species turnover occurring within each river.

The same Jaccard’s distance matrices used in the cluster analysis were also used to evaluate patterns of multivariate beta dispersion \((i.e., \text{beta diversity})\) between assessment periods. Principal coordinate analysis (PCoA) is used to measure and analyze group beta dispersion within predetermined groups of observations (Anderson et al., 2006). In this case, groups represent a regional species pool \((i.e., \text{rivers in the UMRB})\) at two different time periods \((i.e., \text{assessment periods})\). Two separate PCoA ordinations were created using Jaccard’s distance matrices; one for each river and one for river section faunal observations. In the ordinations, historic and recent river observations were grouped by convex hulls, with each hull surrounding a unique group centroid to help visualize dispersion patterns among assessment periods (Maloney et al., 2011). Beta dispersion was directly measured as the distance of each river observation to the group centroid. The use of PCoA is advantageous because it allows the direct measurement of the distance \((i.e., \text{dissimilarity})\) of each independent observation to a group centroid in multivariate space using Euclidean distance, thereby allowing users to perform inferential statistical tests (Anderson et al., 2006). Mean beta dispersions were summarized for each group and permutation tests were performed to test for differences in dispersion between assessment periods. Multivariate beta dispersion analyses were performed using the betadisper and permutest functions from the Vegan and MASS packages in R (R Development Core Team 2011) with an \(\alpha = 0.05\).
RESULTS

Historic trends in species occurrence were assessed for 126 fish species sampled from five mainstem nonwadeable rivers in Iowa (Table 2). Trends describing increases, declines, and no changes in species distribution were confidently determined for 37-80% of species across rivers (Fig. 2A). Although the unknown trends were represented for species in the Maquoketa (63%), Wapsipinicon (35%), and Iowa (36%) rivers, the majority of species assessed in these rivers exhibited changes in their occurrence largely described by either increases or declines. With the exception of the Maquoketa River, occurrence trends were confidently determined for the majority (≤ 64%) of species from the other study rivers. Species with unknown trends were primarily composed of new native species detections, including 14 native fishes (i.e., native to Iowa) that were recently detected among rivers. Fish distributions have increased for 16-26% of species among study rivers. In particular, the Cedar River exhibited the greatest percentage of fish species with increased occurrence (Fig. 2A). The percentages of species with a declining distribution varied from 3-47% among rivers. The highest percentage of species declines occurred in the Des Moines River, whereas the lowest percentage (i.e., only two species) occurred in the Maquoketa River. Species exhibiting no historical change in distribution accounted for 17-27% of species among rivers. Of all the study rivers, the Wapsipinicon River exhibited the highest percentage of species exhibiting no temporal change in occurrence.

Historic trends of fish SGCN occurrence were unlike the trends observed using all fish species. Very few fish SGCN exhibited increasing trends or trends show no change between assessment periods (Fig. 2B). High percentages of fish SGCN showed declines in
the Des Moines, Iowa, Cedar, and Wapsipinicon rivers. Of these rivers, the Des Moines River exhibited the largest percentage (63%) of declining species. Additionally, over 40% of fish SGCN exhibited unknown trends in the Maquoketa, Wapsipinicon, Cedar, and Iowa rivers. In the Maquoketa River, 95% of fish SGCN had an unknown change in distribution, thereby prohibiting temporal trend determination for these SGCN.

Fifteen families represented declining species and ten families represented species increasing in occurrence in more than one river (Fig. 3). Of the families with declining species, five families exhibited no species with increased occurrence, including Amiidae, Anguillidae, Atherinopsidae, Fundulidae, and Gasterosteidae. The greatest percentages of species declines per family were observed for cyprinids (40-53%), centrarchids (6-50%), and percids (0-17%). Families with species exhibiting only increased occurrence were Clupeidae, Moronidae, and Sciaenidae. The greatest percentages of species with increased occurrence per family were observed for cyprinids (29-58%), catostomids (5-32%), and centrarchids (11-18%).

Trends in species occurrence described by habitat traits were highly variable (Fig. 3). The greatest declines in all rivers were among species dependent on backwater habitats. At least 38% of the declining species across all rivers were backwater specialists. Additionally, high percentages (at least 17% across rivers) of declines were also explained by species dependent on free-flowing, riverine habitats. Although high percentages of fluvial specialists declined in most rivers, at least 21% of fluvial species increased in distribution in all rivers. The largest percentages of species with increased occurrence among rivers were characterized by species with generalized habitat preferences. Specifically, over 50% of species that increased in occurrence in all rivers were habitat generalists.
Trends among reproductive guilds were variable across rivers (Fig. 4). The most consistent patterns were represented by phyophilic spawners. Phyophilic spawners characterized the largest percentage of declining species in all rivers (≥ 27% of declining species). To a lesser extent, lithophilic spawners represented at least 17% of the declining species in the Des Moines, Iowa, and Wapsipinicon rivers. High percentages of species with increased occurrence were explained by complex nesters and pelagophilic fishes. Of the species increasing in occurrence, at least 32% were nesting spawners and 12% were pelagophilic spawners.

Trends in species occurrence varied among trophic guilds (Fig. 4). General invertivores represented the greatest percentages of species declining in all rivers, except the Maquoketa River. Excluding the Maquoketa River, at least 27% of all species declining in distribution were general invertivores. Although only 9% of species declines were explained by herbivorous-detritivorous fishes, the majority of herbivore-detritivores have declined. The highest percentages of species increasing in occurrence were represented by carnivores (8-16%), omnivores (12-22%), and benthic invertivores (0-29%). Although some planktovorous fishes explained a low percentage of the species increasing in occurrence, planktivores only increased in occurrence and exhibited no patterns of decline.

Several spatiotemporal patterns in faunal similarity were apparent among rivers (Fig. 5; upper panel). Two main clusters characterized a temporal division among riverine fish assemblages. Bootstrap analysis of the cluster data indicated significance of a historic (AU = 0.92) and recent cluster (AU = 0.95). The historic cluster described a significant faunal affinity among fish assemblages in the Des Moines, Cedar, and Iowa rivers. The recent cluster described a significant faunal affinity among fish assemblages from Des Moines,
Cedar, Iowa, Wapsipinicon, and Maquoketa rivers. The historic fish assemblage from the Wapsipinicon River was also included in the recent cluster. Excluding the Maquoketa and Wapsipinicon rivers, differences between clusters indicated a change in species over time in the Des Moines, Cedar, and Iowa rivers. The historic assemblage in the Maquoketa River exhibited only a low similarity with the ichthyofauna in the historic cluster while the historic and recent fish assemblages in the Wapsipinicon River were highly similar.

Cluster analysis of species composition in HUC-8 river sections primarily described a spatial pattern of faunal similarity (Fig. 5; lower panel). The cluster analysis contained two main clusters which exhibited differences among upstream and downstream HUC-8 fish assemblages. The first cluster described downstream similarities in fish assemblages among HUC-8 river sections near or directly connected to the Mississippi River. These river sections included the lower Des Moines, lower Iowa, lower Cedar, lower Wapsipinicon, and the Red Rock section of the Des Moines River. The first cluster also contained the historic fish assemblage observation from the Maquoketa River (i.e., only one HUC-8 was present). The second cluster reflected similar fish assemblages among upstream HUC-8 river sections. These upstream HUC-8 river sections were largely separated from the Mississippi River with the exception of the Maquoketa River. Upstream river sections were all upper and middle HUC-8 sections from the Des Moines, Iowa, Cedar, and Wapsipinicon rivers. Bootstrap analysis of the cluster data confirmed high fidelity of cluster membership among downstream (AU = 0.90) and upstream HUC-8 river sections (AU = 0.90). The Maquoketa River had a variable affinity for upstream and downstream fish assemblages which differed in each assessment period.
Historic changes in species composition (i.e., turnover) measured by percent Jaccard’s dissimilarity, varied within and among rivers (Fig. 6). The largest temporal change in fish assemblages within rivers occurred in the Maquoketa River (47.5%) followed by the Iowa (43%), Des Moines (37%), and Cedar (28%) rivers (Fig. 6A). Compared to the other rivers, the fish assemblage in the Wapsipinicon River exhibited the smallest change (19.3%). Within rivers, the largest temporal changes in fish assemblages occurred in downstream HUC-8 river sections whereas upstream river sections changed the least (Fig. 6B). Except for the Maquoketa River, downstream fish assemblages exhibited the largest change in the Des Moines River (70.8%), followed by the Wapsipinicon (52.2%) and Cedar (48.8%) rivers. Although the downstream fish assemblage in the Iowa River exhibited a slightly higher turnover (54.9%) than upstream river sections (46.3-51.5%), turnover was fairly similar among downstream and upstream HUC-8 river sections. Differences in species turnover among upstream and downstream HUC-8 observations indicated that changes in species composition occurring at the river scale were largely driven by compositional changes occurring in downstream fish assemblages in the Des Moines, Wapsipinicon, and Cedar rivers.

Principle coordinate analysis characterized differences in multivariate dispersion among river faunas from each assessment period (Fig. 7A). Historic river faunas exhibited higher and more variable values of beta dispersion in rivers (mean = 0.25; SD = 0.09) than recent fish faunas (mean = 0.17; SD = 0.03). A permutation test confirmed a statistical difference in beta dispersions between assessment periods ($F_{1, 8} = 3.54, P = 0.04$). Therefore, changes in beta dispersion indicated that river ichthyofauna have become increasingly similar
over time. Although a significant decrease in beta dispersion was observed, the change in mean beta dispersion indicated only slight temporal increase in faunal similarity.

Principle coordinate analysis characterized minor variation by multivariate beta dispersion among HUC-8 ichthyofauna from each assessment period (Fig. 7B). Historic faunal observations in HUC 8 river sections exhibited slightly higher and more variable values of multivariate beta dispersion (mean = 0.35; SD = 0.08) compared to recent faunal observations (mean = 0.31; SD = 0.06). A permutation test indicated no difference between mean values of HUC-8 multivariate beta dispersion ($F_{1, 24} = 2.03$, $P = 0.15$) in each assessment period. Therefore, patterns of beta diversity among ichthyofauna in HUC-8 river sections have not changed substantially over time.

**DISCUSSION**

Historic changes in ichthyofauna were apparent in Iowa’s nonwadeable rivers. Temporal changes have occurred in all rivers, yet the magnitude of assemblage shifts varied by river and spatial position in the river. Results of the cluster analysis suggested that species composition has changed significantly in the Des Moines, Cedar, and Iowa rivers. Although changes in species composition have occurred in the Wapsipinicon and Maquoketa rivers, these changes were minor or ambiguous. Shifts in species composition reflect declines of groups of specialist fishes and increased occurrence of groups of species with generalized functional and ecological traits. In particular, declines of specialist fishes (e.g., backwater and fluvial specialists) suggested the loss and (or) alteration of important riverine and floodplain habitats.
The decline of many habitat specialists was likely due to widespread increases in anthropogenic disturbances in Iowa’s landscape and rivers. In particular, decline of historically occurring backwater specialist fishes (e.g., golden shiner Notemigonus crysoleucas, tadpole madtom Noturus gyrinus, and brook silverside Labidesthes sicculus) across rivers is likely due to channelization, destruction of riparian and floodplain habitat, and various effects from altered flow regimes (Menzel, 1981; Burr and Page, 1986; Sparks, 1995; Armitage and Rank, 2009). After the loss of many unique floodplain habitats via draining practices, remnant floodplain habitats were later affected by channelization and sedimentation (Menzel, 1981, 1983). Modification of river channels in the late 1800s contributed to rapid loss of habitat heterogeneity and connectivity to off-channel habitats around the turn of the 20th century. If connections to floodplain habitats are not lost by channelization, then increased sedimentation can speed the geomorphic processes by either disconnecting or filling off-channel habitats (Sparks, 1995; Bunn and Arthington, 2002). Many backwater species have also declined due to the loss of aquatic macrophytes. Highly-specialized fishes in floodplain and off-channel habitats are often phytophilic species (e.g., bowfin Amia calva, blacknose shiner Notropis heterolepis, and banded killifish Fundulus diaphanous) that pursue floodplain habitats with high water clarity and abundant aquatic macrophyte substrates for spawning. The distribution and abundance of aquatic macrophytes is likely reduced due to changes in the flow regime or from the effect of increased turbidity in the water column (Rogers and Theiling, 1999; Bunn and Arthington, 2002).

In downstream habitats, the decline of both backwater and fluvial specialists characterized the most evident temporal shifts in species composition occurring within rivers. Using different methods Pierce et al., (In Press) demonstrated similarly large differences
between upstream and downstream fish assemblages in recent fish collections in Iowa. Downstream temporal turnover reflected species declines-extirpations, expansions, and recent detections (Roberts and Hitt, 2010). The local extirpations of 13 backwater species (e.g., blacknose shiner and black bullhead *Amiurus melas*) and 8 fluvial specialists (e.g., hornyhead chub *Nocomis biguttatus* and blackside darter *Percina maculata*) in downstream river sections potentially indicates a historic reduction in habitat diversity (Roberts and Hitt, 2010). Although much of the physical structure of floodplain habitat remains relatively intact, losses in downstream fish biodiversity may reflect a reduction in thermal heterogeneity (Ward and Stanford, 1995). Floodplain habitats in braided and meandering rivers can contain a variety of temperature refugia able to support a high diversity of fishes (Ward and Stanford, 1995).

Although fluvial specialist and dependent species exhibited declines in all study rivers, declines were the most evident in the Des Moines River. Declines and extirpations of fluvial specialists (e.g., common shiner *Luxilus cornutus* and black redhorse *Moxostoma duquesni*) described the primary shift in fish assemblage structure in the Des Moines River. Of all interior rivers in Iowa, the Des Moines River basin has exhibited the largest increase in water storage capacity in impoundments since the 1950s (Falcone *et al.* 2010). Impoundments alter riverine environments by transforming a lotic system into an artificial lentic environment and by affecting local hydrology through changes in stream flow upstream and downstream of dams (Dynesius and Nilsson, 1994; Poff *et al.*, 1997). The reduction of flowing water and the accumulation of fine sediments potentially explains the decline of fluvial fishes with lithophilic spawning strategies. Similarly, Guenther and Spacie (2006) observed declines of lithophilic spawners due to sedimentation upstream of
impoundments in the Wabash River. Increased sedimentation has been shown to considerably alter the trophic structure of local fish assemblages in many Midwestern lotic systems exhibiting hydrologic disturbance (Menzel, 1981, 1983; Poff and Allan, 1995). Moreover, sedimentation has been attributed to the reduction in trophic diversity in fish assemblages in Midwestern lotic systems (Berkman and Rabeni, 1987). The findings of our study agree with Berkman and Rabeni (1987) and others (e.g., Karr et al., 1985; Guenther and Spacie, 2006; Palić et al., 2007; Gido et al., 2010) where specialized invertivorous and herbivorous fishes have declined in altered fluvial environments and been replaced by habitat generalists with piscivorous, planktivorous, or omnivorous feeding strategies (e.g., habitat generalist and facultative reservoir species; Karr et al., 1985; Falke and Gido, 2006).

Recently, numerous studies have observed losses of fish biodiversity by identifying patterns in biotic homogenization among lotic fish assemblages throughout North America (e.g., Rahel, 2010). Researchers have commonly observed habitat degradation facilitating the underlying mechanisms causing the loss of beta diversity: the temporal replacement of specialized native fishes by cosmopolitan fishes (Scott and Helfman, 2001; Olden and Poff, 2003). Before evaluating changes in Iowa’s riverine fish assemblages, we hypothesized that there would be a loss of beta diversity (i.e., increased similarity) among fish assemblages characterized in rivers and HUC-8 river sections over time. Results of the analysis of multivariate beta dispersion failed to support this hypothesis. Although a significant decrease in multivariate dispersion occurred when assessing temporal patterns of beta diversity at the river scale, this increase in faunal similarity was small and largely influenced by few historic samples in the Maquoketa River. Certainly, Iowa’s riverine ichthyofauna exhibited a slight increase in faunal similarity due to the loss of spatially-distinct native fish
distributions and increased occurrence of nonnative and generalist fishes (e.g., sports fishes, exotic species, and translocated-native species; Bernstein and Olson, 2001); however, these changes were spatially and temporally dynamic and obscured clear patterns of homogenization.

This study examined historic changes in the fish assemblages of five large mainstem rivers in Iowa. The use of historical data has provided valuable perspectives about the spatiotemporal dynamics of fish assemblages. Specifically, trends in fish assemblage structure provide valuable information on the status of riverine fishes to managers and conservation planners. The low percentages of unknown trends and clear changes in faunal similarity suggest that we are developing a better understanding of faunal changes occurring in the Des Moines, Iowa, Cedar, and Wapsipinicon rivers. However, faunal changes occurring in the Maquoketa River are uncertain, largely due to historic sampling artifacts (i.e., low sample size). Additionally, these results identify conservation priorities, particularly on the rivers exhibiting the largest fish assemblage shifts. Similarly, declines of specific groups of species (i.e., backwater dependents, phytophilic spawners, fluvial specialists) suggest that specific habitats and resources have been altered and provide guidance for management and conservation. Conservation efforts should continue to focus on understanding factors influencing fish assemblages and their role in affecting the overall ecological condition of riverine ecosystems.

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ANDERSON, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. 


ARMITAGE, B. J. AND E. T. RANKIN. 2009. An assessment of threats to the biological 
condition of the Wabash River aquatic ecosystem of Indiana. The Nature 
Conservancy, Indianapolis, Indiana.


Wisconsin.


BERNSTEIN, N. P. AND J. R. OLSON. 2001. Ecological problems with Iowa's invasive and 

BUNN, S. E. AND A. H. ARTHINGTON. 2002. Basic principles and ecological consequences of 


Gelwicks, G. T. 2006. Evaluation of the importance of specific in-stream habitats to fish populations and the potential for protecting or enhancing Iowa’s interior rivers resources (F-160-R). Iowa Department of Natural Resources, Federal Aid to Fish Restoration, Annual Performance Report, Des Moines.


Table 1. Basin, riparian, and mainstem anthropogenic impacts characterized through land use and instream development in five non-wadeable river drainages in Iowa.

<table>
<thead>
<tr>
<th>River</th>
<th>Drainage (km²)</th>
<th>Urban (%)</th>
<th>Agriculture (%)</th>
<th>Urban (%)</th>
<th>Agriculture (%)</th>
<th>Modified channel length (%)</th>
<th>No. dams</th>
<th>Change in dam storage (megaliters)</th>
<th>Change in no. dams</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maquoketa River</td>
<td>4808.6</td>
<td>6.0</td>
<td>75.3</td>
<td>7.1</td>
<td>40.6</td>
<td>18.9</td>
<td>7</td>
<td>1.5</td>
<td>8</td>
</tr>
<tr>
<td>Wapsipinicon River</td>
<td>6479.6</td>
<td>7.4</td>
<td>80.5</td>
<td>6.5</td>
<td>42.5</td>
<td>35.3</td>
<td>10</td>
<td>0.8</td>
<td>4</td>
</tr>
<tr>
<td>Cedar River</td>
<td>20050.5</td>
<td>9.1</td>
<td>80.4</td>
<td>10.6</td>
<td>34.2</td>
<td>65.9</td>
<td>9</td>
<td>3.4</td>
<td>45</td>
</tr>
<tr>
<td>Iowa River</td>
<td>32429.9</td>
<td>8.5</td>
<td>79.3</td>
<td>9.7</td>
<td>20.3</td>
<td>49.7</td>
<td>8</td>
<td>53.4</td>
<td>80</td>
</tr>
<tr>
<td>Des Moines River</td>
<td>37141.9</td>
<td>7.1</td>
<td>78.9</td>
<td>8.7</td>
<td>44.6</td>
<td>64.5</td>
<td>10</td>
<td>94.5</td>
<td>459</td>
</tr>
</tbody>
</table>
Table 2. Estimated percent occurrence (± 95% confidence interval) of fish species sampled in the Des Moines, Iowa, Cedar, Wapsipinicon, and Maquoketa rivers, during the historic (H; 1884-1969) and recent (R; 1990-2011) assessment period. Occurrence measured as percent of river segments a species was present relative to the number of river segments sampled (n) in each river, from each assessment period.

<table>
<thead>
<tr>
<th>Family and species</th>
<th>Scientific name</th>
<th>Cedar</th>
<th>Des Moines</th>
<th>Iowa</th>
<th>Maquoketa</th>
<th>Wapsipinicon</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>H (n=24)</td>
<td>R (n=34)</td>
<td>H (n=34)</td>
<td>R (n=28)</td>
<td>H (n=16)</td>
</tr>
<tr>
<td>Petromyzontidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern brook lamprey&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Ichthyomyzon fossor</em></td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Silver lamprey&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Ichthyomyzon unicuspis</em></td>
<td>—</td>
<td>—</td>
<td>3(0.6)</td>
<td>0(0.0)</td>
<td>—</td>
</tr>
<tr>
<td>American brook lamprey&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Lampetra appendix</em></td>
<td>0(0.0)</td>
<td>3(0.6)</td>
<td>—</td>
<td>—</td>
<td>0(0.0)</td>
</tr>
<tr>
<td>Acipenseridae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shovelnose sturgeon&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Scaphirhynchus platyurus</em></td>
<td>4(1.1)</td>
<td>27(1.5)</td>
<td>0(0.0)</td>
<td>7(1.0)</td>
<td>0(0.0)</td>
</tr>
<tr>
<td>Polyodontidae</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Paddlefish&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Polyodon spathula</em></td>
<td>4(1.0)</td>
<td>3(0.6)</td>
<td>3(0.6)</td>
<td>4(0.7)</td>
<td>6(1.8)</td>
</tr>
<tr>
<td>Lepisosteidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spotted gar</td>
<td><em>Lepisosteus oculatus</em></td>
<td>—</td>
<td>—</td>
<td>0(0)</td>
<td>7(1.0)</td>
<td>—</td>
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<tr>
<td>Longnose gar&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Lepisosteus osseus</em></td>
<td>4(1.1)</td>
<td>18(1.4)</td>
<td>12(1.1)</td>
<td>14(1.4)</td>
<td>6(1.8)</td>
</tr>
<tr>
<td>Shortnose gar</td>
<td><em>Lepisosteus platostomus</em></td>
<td>4(1.1)</td>
<td>24(1.5)</td>
<td>3(0.6)</td>
<td>21(1.6)</td>
<td>6(1.9)</td>
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<tr>
<td>Amiidae</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bowfin&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Amia calva</em></td>
<td>12(1.7)</td>
<td>0(0.0)</td>
<td>—</td>
<td>—</td>
<td>12(2.5)</td>
</tr>
<tr>
<td>Hiodontidae</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Goldeye&lt;sup&gt;5&lt;/sup&gt;</td>
<td><em>Hiodon aloidos</em></td>
<td>0(0.0)</td>
<td>3(0.6)</td>
<td>27(1.6)</td>
<td>14(1.3)</td>
<td>0(0.0)</td>
</tr>
<tr>
<td>Mooneye</td>
<td><em>Hiodon tergisus</em></td>
<td>8(1.4)</td>
<td>9(1.0)</td>
<td>0(0)</td>
<td>22(1.6)</td>
<td>0(0.0)</td>
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<tr>
<td>Anguillidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>American eel&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Anguilla rostrata</em></td>
<td>12(1.7)</td>
<td>0(0.0)</td>
<td>21(1.4)</td>
<td>4(0.7)</td>
<td>6(1.8)</td>
</tr>
<tr>
<td>Clupeidae</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Skipjack herring</td>
<td><em>Alosa chrysochloris</em></td>
<td>—</td>
<td>—</td>
<td>0(0.0)</td>
<td>4(0.7)</td>
<td>—</td>
</tr>
<tr>
<td>Gizzard shad</td>
<td><em>Dorosoma cepedianum</em></td>
<td>38(2.4)</td>
<td>41(1.7)</td>
<td>15(1.3)</td>
<td>47(2.0)</td>
<td>13(2.5)</td>
</tr>
<tr>
<td>Cyprinidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central stoneroller</td>
<td><em>Campostoma anomalum</em></td>
<td>25(2.3)</td>
<td>27(1.6)</td>
<td>23(1.5)</td>
<td>4(0.7)</td>
<td>44(3.7)</td>
</tr>
<tr>
<td>Largescale stoneroller&lt;sup&gt;3&lt;/sup&gt;</td>
<td><em>Campostoma oligolepis</em></td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0(0.0)</td>
</tr>
<tr>
<td>Goldfish&lt;sup&gt;1&lt;/sup&gt;</td>
<td><em>Carassius auratus</em></td>
<td>4(1.1)</td>
<td>9(1.0)</td>
<td>—</td>
<td>—</td>
<td>0(0.0)</td>
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<tr>
<td>Lake chub</td>
<td><em>Coho salmon</em></td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>6(1.9)</td>
</tr>
<tr>
<td>White amur&lt;sup&gt;1&lt;/sup&gt;</td>
<td><em>Ctenopharyngodon idella</em></td>
<td>0(0.0)</td>
<td>9(1.0)</td>
<td>0(0.0)</td>
<td>11(1.2)</td>
<td>0(0.0)</td>
</tr>
<tr>
<td>Species</td>
<td>Adult g</td>
<td>Juvenile g</td>
<td>Length</td>
<td>Females dr</td>
<td>Males dr</td>
<td>Eggs</td>
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<tr>
<td>---------------------------------</td>
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</tr>
<tr>
<td>Red shiner Cyprinella lutrensis</td>
<td>2(2.1)</td>
<td>6(0.8)</td>
<td>21(1.3)</td>
<td>18(1.5)</td>
<td>6(1.8)</td>
<td>—</td>
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<tr>
<td>Spotfin shiner Cyprinella spilotra</td>
<td>29(2.4)</td>
<td>88(1.1)</td>
<td>33(1.7)</td>
<td>54(1.9)</td>
<td>25(3.1)</td>
<td>77(1.4)</td>
</tr>
<tr>
<td>Common carp</td>
<td>42(2.6)</td>
<td>97(0.6)</td>
<td>76(1.5)</td>
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Table 2. Continued (see p. 38 for heading)
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<th>Feeding</th>
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<td>(2.4)</td>
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<td>(1.7)</td>
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<td>(1.6)</td>
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<td>(2.1)</td>
<td><strong>65</strong></td>
<td>(1.7)</td>
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### Table 2. Continued (see p. 38 for heading)

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<td>Brook trout ⁵</td>
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<td>Percidae ⁵</td>
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<td>Width</td>
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<td>Iowa darter (Etheostoma exile)</td>
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<td>0(0.0)</td>
<td>9(1.0)</td>
</tr>
<tr>
<td>Fantail darter (Etheostoma flabellare)</td>
<td>13(1.7)</td>
<td>24(1.5)</td>
<td>15(1.2)</td>
</tr>
<tr>
<td>Least darter (Etheostoma microperca)</td>
<td>4(1.0)</td>
<td>0(0.0)</td>
<td>—</td>
</tr>
<tr>
<td>Johnny darter (Etheostoma nigrum)</td>
<td>13(2.5)</td>
<td>64(1.7)</td>
<td>26(1.6)</td>
</tr>
<tr>
<td>Orangenthroat darter (Etheostoma spectabile)</td>
<td>—</td>
<td>—</td>
<td>0(0.0)</td>
</tr>
<tr>
<td>Banded darter (Etheostoma zonale)</td>
<td>12(1.7)</td>
<td>44(1.7)</td>
<td>21(1.4)</td>
</tr>
<tr>
<td>Yellow perch (Perca flavescens)</td>
<td>4(1.0)</td>
<td>15(1.2)</td>
<td>18(1.4)</td>
</tr>
<tr>
<td>Northern logperch (Percina caprodes)</td>
<td>8(1.4)</td>
<td>56(1.7)</td>
<td>12(1.1)</td>
</tr>
<tr>
<td>Gilt darter (Percina evides)</td>
<td>4(1.1)</td>
<td>0(0.0)</td>
<td>3(0.6)</td>
</tr>
<tr>
<td>Blackside darter (Percina maculata)</td>
<td>13(1.7)</td>
<td>24(1.5)</td>
<td>30(1.5)</td>
</tr>
<tr>
<td>Slenderhead darter (Percina phoxocephala)</td>
<td>12(1.7)</td>
<td>74(1.6)</td>
<td>18(1.4)</td>
</tr>
<tr>
<td>River darter (Percina shumardi)</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>S~ager (Stizostedion canadense)</td>
<td>8(1.5)</td>
<td>15(1.3)</td>
<td>3(0.6)</td>
</tr>
<tr>
<td>Walleye (Stizostedion vitreum)</td>
<td>21(2.0)</td>
<td>77(1.5)</td>
<td>59(1.7)</td>
</tr>
<tr>
<td>Sciaenidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freshwater drum (Aplodinotus grunniens)</td>
<td>8(1.4)</td>
<td>41(1.7)</td>
<td>27(1.6)</td>
</tr>
</tbody>
</table>

*Species of greatest conservation need  ^ Non-native to Iowa
Figure 1. Map of the study river systems (top) in Iowa and their corresponding 8-digit hydrologic unit code basins (HUC-8): Upper, Middle, Red Rock (Lake), and Lower. The lower panel illustrates the spatial distribution of mainstem sampling sites in the Des Moines, Iowa, Cedar, Wapsipinicon, and Maquoketa rivers, during the historic (1884-1969) and recent (1990-2011) assessment periods.
Figure 2. Percentage of all species (A) and species of greatest conservation need (B) exhibiting temporal trends in occurrence in the Des Moines, Iowa, Cedar, Wapsipinicon, and Maquoketa rivers of Iowa.
Figure 3. Increasing and declining trends in occurrence of fish described through percent of species represented in each family (left panels) and habitat-use guild (right panels) for non-wadeable river systems in Iowa. Families and habitat-use guilds were included if at least one species exhibited trends in more than one river or if more than one species exhibited change in only one river system.
Figure 4. Increasing and declining trends in occurrence of fish described through percent of species represented in each reproductive (left panels) and trophic guild (right panels) for non-wadeable river systems in Iowa. Reproductive and trophic guilds were included if at least one species exhibited changes in more than one river or if more than one species exhibited change in only one river.
Figure 5. Cluster dendrograms describing similarities and differences among historic (bold-italic font) and recent (regular font) fish assemblages in rivers (top dendrogram) and 8-digit basin (HUC-8) delimited river sections (bottom dendrogram) using Jaccard’s distance matrices for non-wadeable river systems in Iowa.
Figure 6. Species turnover described by Jaccard’s percent dissimilarities in rivers (A) and 8-digit basin (HUC-8) delimited river sections (B) from historic (1884-1969) to recent (1990-2011) assessment periods for non-wadeable river systems in Iowa.
Figure 7. Principle coordinate analysis ordinations comparing multivariate beta dispersion among fish assemblage observations in rivers (A) and 8-digit basin (HUC-8) delimited river sections (B), between historic (1884-1969) and recent (1990-2011) assessment periods for non-wadeable rivers in Iowa.
CHAPTER 3. ANTHROPOGENIC DISTURBANCE AND ENVIRONMENTAL ASSOCIATIONS WITH FISH ASSEMBLAGE STRUCTURE IN TWO NONWADEABLE RIVERS

A manuscript to be submitted for publication in River Research and Applications.

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ABSTRACT

Nonwadeable rivers are unique ecosystems that support high levels of fish biodiversity. Although riverine fish assemblages have been studied in the past, there is an incomplete understanding of how fish assemblages respond to both natural and anthropogenic influences in rivers. The purpose of this study was to evaluate associations between fish assemblage structure and landscape-scale, dam-related, and reach-scale environmental 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, trait abundance (e.g., catch rate of tolerant species), and trait composition (e.g., percentage of tolerant species). Variance

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partitioning from partial CCAs identified that reach-scale environmental characteristics contributed the majority of variance in fish assemblages described in the CCA models. Relative to landscape characteristics, dams explained a considerable amount of variation in the CCAs. Among the reach-scale variables, mean annual discharge was consistently selected in CCA models and accounted for the majority of explained variance among reach-scale variables. Dominant discharge patterns suggested that fish assemblages were primarily structured longitudinally corresponding with changes in discharge.

KEY WORDS: multiple spatial-scale, longitudinal structure, flow variation, dams

INTRODUCTION

The occurrence and abundance of fishes are influenced by numerous abiotic and biotic factors that vary throughout time and space (Matthews, 1998; Jackson et al., 2001). Large-scale factors such as geography, geology, climate, landscape characteristics, and natural barriers typically regulate the dispersal and spatial distribution of fish species (Matthews, 1998; Marsh-Matthews and Matthews, 2000); whereas, local-scale factors such as habitat structure (Gorman and Karr, 1978) and biotic interactions tend to determine the abundance and function of fishes in an aquatic ecosystem (Grossman et al., 1982). To predict and understand patterns of fish assemblage structure, a multiple-scale approach must be used (Allan, 2004; Hoeinghaus et al., 2007; Sindt et al., 2012). In particular, concepts such as faunal and landscape filters have successfully demonstrated the link between fish assemblage structure and environmental characteristics operating at multiple spatial and temporal scales (Poff, 1997; Quist et al., 2005). Due to widespread anthropogenic impacts
on aquatic ecosystems and the rapid decline of many fish species, it is important to understand the scale and magnitude of human disturbance relative to other environmental factors (Allan, 2004; Hughes et al., 2005; Burkhead, 2012).

Ecological processes exhibit clinal changes along a river or stream allowing for predictable spatial patterns in ecosystem structure and function (Vannote et al., 1980; Funk et al., 1989). At a large geographic extent, local fish assemblages generally exhibit longitudinal (i.e., upstream to downstream) trends in species richness and composition along the length of a river (Sheldon, 1968; Rahel and Hubert, 1991; Matthews, 1998). Downstream changes in fish assemblages typically reflect changes in river size, habitat structure, environmental stability, and source-sink dynamics (Sheldon, 1968; Schlosser, 1990; Roberts and Hitt, 2010; McGarvey, 2011). Many forms of human disturbance (e.g., dams) can alter spatial patterns in lotic ecosystems (Ward and Stanford, 1995). Although dams and other disturbances create discontinuities in river ecosystems, consistent longitudinal patterns in fish assemblage structure often emerge in impounded systems when examined across large geographic extents (Chick et al., 2006, Miranda et al., 2008). Fish assemblages may exhibit simultaneous relationships with the position and number of dams along a river's course, suggesting the potential importance of both factors but obscuring the relative influence of each (Pierce et al., In Press).

Lotic systems, particularly in the Midwest, have a long history of disturbance and degradation from cumulative human activities (Karr et al., 1985). Dams are considered one of the most pervasive disturbances affecting lotic ecosystems (Dynesius and Nilssen, 1994; Hughes et al., 2005). Dams interrupt dynamic ecosystem processes (Ward and Stanford, 1995), alter natural flow variability (Poff and Allan, 1995; Poff et al., 1997), transform
habitats upstream and downstream of dams (Kinsolving and Bain, 1993; Quist et al., 2004; Guenther and Spacie, 2006), and act as dispersal barriers (Freeman et al., 2003; Santucci et al., 2005). Because dams have an overarching influence on local habitat characteristics and fish dispersal, they are considered influential at an intermediate spatial-scale (Weigel et al., 2006; Falke et al., 2006; Wang et al., 2011).

Large rivers are complex aquatic ecosystems that provide a variety of important resources, yet there is still an incomplete understanding about large river ecology and how large river ecosystems respond to anthropogenic disturbance (Sparks, 1995; Allan, 2004). Previous studies in large river fish ecology have typically focused on concepts of biotic integrity (Lyons, 2001) or have examined habitat relationships with only a fraction of a local fish assemblage (Mendejczyk et al., 1998). Only a few studies have attempted to comprehensively observe fish assemblages and their correspondence to habitat (e.g., Barko et al., 2004; Neebling and Quist, 2010) or disturbance (e.g., Eitzmann and Paukert, 2010).

Recent use of comprehensive fish sampling techniques in nonwadeable rivers has improved our understanding of local and regional fish assemblages in large rivers (Herzog et al., 2005; Neebling and Quist, 2010). Currently, the status of riverine fish assemblages across North America is generally poor and in some cases unknown (Jelks et al., 2008; Burkhead, 2012). To improve the conservation status of riverine fishes, it is critical to understand how fishes are influenced by dynamic environments (Sparks, 1994; Hughes et al., 2005; Burkhead, 2012).

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 increase our understanding of how anthropogenic disturbance and natural
environmental variation operate at different spatial-scales to influence patterns of fish assemblage structure and function. To accomplish this objective, fish and environmental data were collected from the Cedar and Iowa rivers in Iowa. Taxonomic and species traits (e.g., life history strategies and habitat-use guilds) were used to describe a suite of fish assemblage and functional responses to environmental factors. We then assessed the relative influence from environmental variables at each spatial scale (i.e., reach, intermediate-dam, and landscape) to explain prominent patterns in fish assemblage structure in the two river systems. Additionally, by partitioning variance in fish assemblages by spatial-scale, we expected to discern and identify important sources of environmental variation associated with anthropogenic disturbance. In particular, we hypothesized that dams would be as important as landscape variables in influencing fish assemblage structure.

**METHODS**

*Study area and survey design*

This study was performed 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 km²). 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, 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, a systematic sampling design was used to assign sampling reaches along each river profile (McGarvey, 2011). Twenty-two nonwadeable sampling reaches (3.9 km in length) were systematically established at 36 km intervals along the lengths of the Cedar and Iowa rivers. Eleven additional sampling reaches were randomly placed 0-10 km above impoundments or below dams to further assess influence of dams on fish assemblages.

*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 (2,500 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 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 3,000 W. Boat-mounted electrofishing was performed with an operator and two netters using dipnets (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. Trawling 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 drop ratio (max 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 and large-bodied fishes. Design and operation of
Herzog-Missouri trawl can be found in Herzog et al. (2005). Effort for each sampling run was recorded as time electrofished (hours) and distance trawled (meters). 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 solution.

**Environmental data**

At each fish sampling reach, environmental variables were measured and summarized at the reach-scale following Neebling and Quist (2010) who adopted methods used in the U.S. 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), substrate composition, and instream cover were measured at seven evenly-spaced locations along each transect. Depths were measured to the nearest decimeter using a sounding pole. Depths were taken at permanent physical references (e.g., bridge pylon) during fish sampling events to account for change 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). To reduce the number of substrate variables describing substrate composition, substrate
categories were simplified by calculating the percentage of coarse substrates ($\geq 3$ mm) in each reach. Current velocity (m/s) was measured at 60% at depths $< 1.0$ m, and at 20% and 80% of the depth when depths were greater than or equal to 1.0 m using a Marsh-McBirney Flow-Mate 2000 (Marsh-McBirney Inc., Loveland, CO, USA; Fitzpatrick et al., 1998).

Visible instream cover (large woody debris, vegetation, rock debris, artificial debris) was measured as the percent of instream cover along the length of the river transect. Canopy and bank condition were measured at the endpoints of each transect. Overhanging canopy cover was measured as an aerial percentage using a spherical densiometer. Bank condition was measured as the percentage of shoreline rocky rip-rap in each reach (Eitzmann and Paukert, 2010). 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) was measured before and after electrofishing runs using an EC400 ExStik II conductivity meter (Extech Instruments, Nashua, NH, USA). Streamflow was measured as mean annual discharge ($m^3$/s) using Indicators of Hydrologic Alteration (IHA; Richter et al., 1996) with flow data from U.S. Geological Survey (USGS) gaging stations.

Variables associated with dams were derived using a geographical information system (GIS; Arc GIS 9.3, ESRI, Redlands, CA). Data on dams were obtained from a state dam inventory layer available from the Iowa DNR GIS library (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). Spatial characteristics of dams were similar to 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).

Variables associated with landscape characteristics were also estimated using a GIS to describe land cover percentages within local catchments and basins. Methods similar to Rowe et al. (2009) were employed to determine catchment areas and land cover percentages. 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 (i.e., catchment boundaries set by the NHD from digital elevation models). Local catchments describe the landscape (i.e., riparian and valley area) that immediately contributes runoff along the length of the sampling reach. 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. Using a digital elevation model (30 m resolution) joined to a 1:100,000 scale NHD coverage, local catchment areas were delineated for the length of each sampling reach and basins were delineated for the river network upstream of the lower boundary of each sampling reach. Watershed delineation was performed using Arc Hydro tools (available in Arc GIS 9.3, ESRI, Redlands, CA). Land cover raster data were then joined to catchment delineations to calculate land cover percentages from aggregated raster-layers from the 2006 National Land Cover Dataset (Fry et al., 2011). A suite of natural and anthropogenic land cover variables were derived for each catchment including percent agricultural, urban, grassland, wetland, and forest land cover.
Data analysis

Fifty-four candidate environmental variables (26 reach-scale, 7 dam-related, and 16 landscape-scale 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 $r \geq |0.70|$. The least redundant environmental variables with the most ecological relevance were retained among pairs of correlated environmental variables. The final set of environmental variables included 20 variables (TABLE I).

Fish assemblages structure was described using taxonomic (i.e., species) and trait classifications. 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 guild classifications were defined as fish species tolerant, moderately-tolerant, and intolerant to environmental degradation (Wilton, 2004). Fish life history strategies were classified using methods described by Olden and Kenard (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 (Olden and Kenard, 2010; Mimms and Olden, 2012). Life history strategies or endpoints 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; Hoeninghaus et al.,
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; Galat and Zweimuller, 2001).

Relative abundance was calculated as catch-per-unit-effort (CPUE) by species and trait classification, and was calculated separately for electrofishing and trawling data. Electrofishing CPUE was calculated as the number of fish caught per hour of electrofishing (fish/h). Trawling CPUE was calculated as the number of fish caught per 50 m trawl haul. Additionally, fish assemblage structure was described using percent composition of traits (i.e., relative frequency of a specific trait based on species composition; see Pool et al., 2010). Percent composition datasets were created using presence-absence data from both electrofishing and trawling data to determine the percentages of species richness per reach of each tolerance guild, life history strategy, and habitat use guild classification. Before ordinations 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 variation 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). To reduce the influence of rare species, species occurring at less than three reaches (i.e., 10% of reaches) were excluded from analyses (Legendre and Legendre, 1998). Separate CCAs were performed for electrofishing CPUE, trawling CPUE, and trait richness datasets. Canonical correspondence analyses were conducted using a forward-selection procedure with Monte Carlo permutation tests (1,000 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 among selected environmental variables 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 displayed in ordinations using the first two CCA ordination axes. In most cases, the third axis described a limited amount of model variance ($\leq 10\%$ of total variance).

Partial CCAs (pCCA) were used to partition fish assemblage variation explained by environmental variables to determine the relative importance of reach-scale, dam-related, and landscape-scale environmental variables (Weigel et al., 2006). Using the various CCA models, pCCAs were created to partition the total inertia (i.e., $\chi^2$ distance) or total variance in fish assemblages constrained by each set of environmental variables (Legendre and Legendre, 1998). Explained variance ($) was described as the inertia explained by specific environmental characteristics relative to the total constrained inertia (ter Braak and Smilauer, 2002). The relative importance of each set of environmental variables was determined by comparisons of the explained variance percentages among environmental variable sets.
relevant to spatial-scale in each model (i.e., reach-scale, dam-related, and landscape-scale variables). Background variation from environmental variables was removed or conditioned before analyzing the effect of the environmental variables of interest in the CCA model (Legendre and Legendre, 1998). For example, the effects of reach and landscape-scale variables were removed to determine the percentage of fish assemblage variation explained by dams. This process was performed again for individual environmental variables to better understand the specific underlying drivers of fish assemblage structure. Interactions between environmental variable sets were not included because we were only interested in comparing explained variance from environmental descriptors from similar spatial-scales. Percentages of explained variance were compared among taxonomic and trait datasets used to create CCA models. All CCA ordinations and pCCA analyses were performed using the Vegan package in R (R Core Development Team 2011).

RESULTS

A total of 16,033 fish was sampled using boat-mounted electrofishing and 21,201 fish were sampled using benthic trawls in the Cedar and Iowa rivers during the summers of 2010 and 2011. Gizzard shad *Dorosoma cepediamum*, spotfin shiner *Cyprinella spiloptera*, golden redhorse *Moxostoma erythrurum*, and common carp *Cyprinus carpio* dominated the electrofishing catch. Sand shiner *Notropis stramineus*, bigmouth shiner *Notropis dorsalis*, channel catfish *Ictalurus punctatus*, and banded darter *Etheostoma zonale* dominated samples with the trawl. A total of 85 species and two hybrids was sampled (TABLE II). Species richness varied from 26 to 43 species per reach in the Iowa River and 18 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 (e.g., western sand darter *Amocrypta clara* and blue sucker *Cycleptus elongatus*) were not sampled upstream of the Burlington Street Dam on the Iowa River. Similarly, eight species (e.g., Mississippi silvery minnow *Hybognathis nuchalis* and goldeye *Hiodon alosoides*) were not sampled upstream of the Cedar Rapids Milldam on the Cedar River. Five species (e.g., emerald shiner *Notropis atherinoides* and longnose gar *Lepisosteus osseus*) had truncated distributions downstream of the furthest downstream dam in both rivers.

Reach-scale and dam-related environmental characteristics exhibited more variation than characteristics measured at the landscape-scale. Mean annual discharge, bankfull width, conductivity, and percent coarse substrate exhibited the most inter-reach variation among reach-scale characteristics. Mainstem fragment length and distance to downstream dam exhibited the most inter-reach variation among dam-related variables, and the percentage of wetland cover and urban land use in local catchments exhibited the most inter-reach variation among landscape-scale variables. The percentages of agricultural land use measured at the basin scale exhibited less variation than other landscape-scale variables. Several environmental characteristics varied longitudinally, including the percentage of basin agriculture and urban land use, mean bank full width, and mean annual discharge; yet, no major correlation occurred among these variables ($r < |0.70|$). Additionally, indicators of
hydrologic alteration analysis identified higher levels of temporal flow variation at upstream USGS gages (e.g., 05458500-Cedar River at Janesville, annual CV = 1.61; 05451500-Iowa River at Marshalltown, annual CV = 1.51) compared to downstream gages (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 of the variance 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, agricultural land use, and riparian-bank condition. Higher abundances of species in upstream reaches (e.g., golden redhorse, northern pike *Esox lucius*, and common shiner *Luxilus cornutus*) were related to low discharge environments with more canopy cover and increased proportions of basin agriculture. Downstream reaches were characterized by increased discharge, higher proportions of shoreline rip-rap, and lower proportions of basin agriculture. Downstream reaches contained high abundances of “large-river” species (e.g., gizzard shad, white bass *Morone chrysops*, and flathead catfish *Pylodictis olivaris*).

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 connectivity, and substrate composition. This gradient contrasted species associated with increased discharge, increased local wetland connectivity, 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 separated species associated with reaches characterized by higher proportions of upstream basin urbanization (e.g., river shiner *Notropis blennius* and bullhead minnow *Pimephales vigilax*) from species associated with reaches containing higher proportions of basin agriculture (e.g., Johnny darter *Etheostoma nigrum* and bigmouth shiner).

Additionally, a pattern of increased abundance of silver chub *Macrhybopsis storeriana*, shoal chub *M. hyostoma*, and shovelnose sturgeon *Scaphirhynchus platypsygus* in longer mainstem river fragments was identified using a 3-dimensional perspective of ordination space (axes not displayed in Figure 3).

**Trait abundance models**

Tolerance guild abundance was best explained by environmental variables in the electrofishing CCA (72.2% of the total variance) compared to 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 urbanization. Electrofishing CPUE of moderately-tolerant
species was positively associated with the distance to upstream dams and the proportion of instream woody cover. In the trawling CCA, increased abundance of tolerant species was primarily associated with higher proportions of basin agriculture along axis 1. Axis 2 primarily represented a gradient of substrate composition. This axis contrasted a high CPUE of intolerant species in habitats containing coarse substrates from a high CPUE of moderately-tolerant species associated with habitats characterized by fine substrates and to a lesser extent, increased flow heterogeneity (i.e., CV of velocity).

Using life history strategies, 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, which separated abundant equilibrium and periodic strategists in reaches with increased discharge (i.e., discharge and bank full width) and more shoreline rip-rap from opportunistic and opportunistic-equilibrium strategists in reaches with less streamflow and less shoreline rip-rap. Additionally, CPUE of periodic and opportunistic–equilibrium strategists was positively associated with mainstem fragment length. Also, increased electrofishing CPUE of periodic-equilibrium strategists was primarily associated with higher proportions of basin urbanization and increased proportions 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, since substrate composition varied along the same gradient. This gradient separated abundant opportunistic, opportunistic-equilibrium, and periodic-equilibrium strategist in low discharge environments containing
coarse substrates from abundant equilibrium and periodic strategists in high discharge environments containing fine substrates. The trawling CCA also described opportunistic-periodic strategist CPUE as being positively associated with distance to downstream dam and mainstem fragment length; whereas periodic strategist CPUE increased in reaches in smaller, more impounded river fragments.

Habitat-use guild variation was best explained by environmental variation in the trawling CCA (61% of total variation) compared to the environmental constraints in the electrofishing CCA (47.7%). Three environmental variables explained variation in habitat guild CPUE in the electrofishing CCA. Positive associations were identified between proportions of shoreline rip-rap and catch rates of macrohabitat generalists, proportion of overhanging canopy and fluvial-dependent CPUE, and reach distance to downstream dams and fluvial-specialist CPUE. In the trawling CCA, four environmental variables explained variation in habitat-use guild CPUE. Axis 1 represented a gradient of discharge, agricultural land use, and riparian canopy. This gradient contrasted a high CPUE of macrohabitat generalists in reaches with high discharge from high CPUE of fluvial dependents and fluvial specialists in reaches with low discharge, abundant overhanging canopy, and high proportions of upstream agriculture. Additionally, axis 2 represented a gradient of current velocity that separated high CPUE of fluvial specialists in swift-flowing habitats from high catch rates of fluvial-dependent species in slower-flowing habitats.

Trait composition models

Five variables were retained to explain 73.6% of total variation in the tolerance guild composition model (FIGURE 5; top panel). Along axis 1, a high composition of intolerant
species was associated with reaches located in smaller mainstem river fragments with high canopy cover. Conversely, higher compositions of moderately-intolerant species were associated with reaches located in larger mainstem river fragments with low riparian canopy cover. Along axis 2, percent composition of tolerant species was positively related to the proportion of upstream agriculture, while negatively related to the proportion of upstream urbanization and distance to downstream impoundments.

Patterns in life history strategy composition were significantly explained by six environmental variables (72.5% of total variation; FIGURE 5; middle panel). River reaches exhibiting higher proportions of coarse substrates and lower streamflow contained fish assemblages with higher compositions of opportunistic, opportunistic-equilibrium, and periodic-equilibrium strategists. On the other hand, environments with more streamflow were associated with a higher percent composition of periodic and equilibrium strategies. Unique fish assemblages containing higher percentages of opportunistic-periodic strategists were primarily associated with local habitats situated within large mainstem river fragments. Along axis 2, river reaches with high discharge, high proportions of upstream urban land use, and low proportions of woody cover were associated with fish assemblages representing a high 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, deep reaches with shoreline rip-rap exhibited a high composition of macrohabitat generalists. As mean depth and percentage of shoreline rip rap decreased, the percent composition of fluvial specialists increased. Along axis 2, higher
compositions of fluvial dependent species were in reaches situated in larger mainstem river fragments.

*Partitioning model variance*

Partitioned variance indentified from partial CCAs 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 explained variance in almost all of the CCA models. Mean annual discharge was commonly selected in the CCAs and explained most of the model variance relative to other reach-scale characters. Among other reach-scale variables, the proportion of shoreline rip-rap also explained high proportions of fish assemblage variation when selected. The remaining variation explained by the environment characteristics was composed of large-scale explanatory variables. Altogether, landscape-scale environmental characteristics contributed 5.8-47.2% of the explained variance in nine CCA models and were largely represented through the proportion of basin agriculture and urban land use. Dam-related characteristics were also identified in nine CCA models and accounted for 6.2-25.1% of the explained variance in fish assemblage structure (i.e., mainly represented by fragment length and distance to impoundment). Landscape-scale environmental variables outperformed dam-variables in six CCA models, particularly in the tolerance guild CCAs and the CCAs using trawling data. On the other hand, dam-related variables accounted for as much or more of the explained 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, patterns of species occurrence and trait composition were longitudinal in structure. However, spatial patterns of fish assemblages corresponded to changes in reach-scale habitat, which was primarily represented by mean annual discharge. Although these longitudinal patterns emerged through fish assemblage associations with reach-scale habitat (e.g., discharge), other ecological patterns of trait abundance and composition was attributed to environmental variation associated with dams and watershed land use. These results further promote the importance of using multiple spatial-scales when evaluating the cumulative influence of natural environments and anthropogenic disturbances on lotic fish assemblages (Poff, 1997; Weigel et al., 2006; Hoeinghaus et al., 2007; Wang et al., 2010; Sindt et al., 2012).

Row-crop agriculture dominates much of the landscape in the state of Iowa; because of this, row-agriculture exhibited little variation among sampling reaches compared to reach-scale characteristics such as discharge. Consequently, 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 large-scale or regional characteristics on habitats and species distributions (Marsh –Matthews and Matthews, 2000; Hoeinghaus et al., 2007). Our analyses differed, since taxonomic structure was largely influenced by local environmental characteristics. These results agree with the findings 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 local-scale habitat, environmental variation associated with dams and land use were still important determinants of fish assemblages the Iowa and Cedar rivers. In particular, large spatial-scale characteristics explained high proportions of tolerance guild variation and in trawling catch rates (i.e., taxonomic and trait abundance). For instance, patterns of tolerance guilds and benthic fish assemblages (i.e., trawling catch rates) exhibited typical responses to agricultural and urban land use (Wilton, 2004). Nonetheless, large-scale environmental influence was minor compared to 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 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 often exhibited in lotic systems in the western US (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., In Press) 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 small-scale (i.e., every 50 rkm) discharge values are inherently linked to longitudinal zonation patterns of fish assemblages. Zonation patterns tend to be the result a broad habitat type characterized among adjacent river reaches (Matthews, 1998). Recent research from McGarvey (2011) agrees with our findings suggesting that spatial changes in species composition (i.e., replacements) in the Cedar and Iowa rivers follows transitional patterns of discharge among groups of adjacent river reaches with similar habitats (i.e., upstream reaches similarly characterized by lower discharge, increased canopy, and coarse substrates).

Temporal dynamics in streamflow further augmented spatial patterns in discharge and fish assemblages in the Cedar and Iowa rivers. Differences in flow variability provided additional insight about a habitat template linking fish life history strategies and mean annual discharge in the Cedar and Iowa rivers. Specifically, increased discharge in downstream habitats was associated with increased abundance and percent composition of equilibrium strategists; whereas, decreased discharge in upstream river habitats corresponded to increased abundance and percent composition of opportunistic-equilibrium and opportunistic strategists. Life history correspondence to spatial changes in flow magnitude and temporal variation of flow 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 (Winemiller
and Rose, 1992; Hitt and Roberts, 2012). The short life span and fast maturation of opportunistic species allows for a fast recovery and re-colonization in more variable lotic environments that are more prone to flashy disturbance (Schloesser, 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 patterns described by discharge, rip-rap characteristics were also consistently identified as an important reach-scale habitat component in the Cedar and Iowa rivers. Shoreline revetments composed of rip-rap (e.g., rocks, tires) have been shown to increase habitat complexity and fish diversity in large rivers (White et al., 2010; Eitzmann and Paukert, 2010) and have characterized unique patterns in species composition compared to other habitats along channel borders (Mendejczyk et al., 1998). However, rip-rapped shorelines have been associated with poor biological integrity, alteration of channel morphology, and loss of ecosystem function (Lyons, 2005). Recently, White et al. (2010) 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. The Iowa and Cedar rivers exhibit considerably higher heterogeneity in substrate composition and instream cover (e.g., large woody debris) than the Kansas River. Therefore, it is 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 native riverine obligates in our study system. Further research is needed to understand the influence of rip-rap in Iowa’s lotic systems in the upper Mississippi River drainage, particularly to differentiate the influences of instream substrates from rip-rapped habitats on fish assemblages.

Local fish assemblage structure was also influenced by dams and impoundments as has been shown by Pierce et al. (In Press). 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. (In Press) 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. Since 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, compared to local 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 accounted for very small amounts of variation in IBI metrics and other fish traits. Compared to these studies, our study found that dams and impoundments accounted for a larger percentage of fish assemblage variation in both functional trait and taxonomic descriptors. Our study was most similar to Weigel et al. (2006) since both studies assessed nonwadeable rivers, were conducted at similar spatial scales, and used the same dam measures that were not confounded by longitudinal position. Much like the work of Weigel et al. (2006), Wang et al. (2011), and Pierce et al. (In Press), model variation explained by dams may suggest that dams play a considerable role in influencing the taxonomic and functional organization of fish assemblages in Iowa’s nonwadeable rivers.

Several 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 needed for the persistence of pelagic spawning minnows (i.e., silver chub and shoal chub) in rivers of the Great Plains. Similarly, Pool et al. (2011) found that small fragments between dams created unfavorable hydrologic conditions to 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 et al. (2006) described a similar pattern in Kansas rivers where high abundance of facultative reservoir species exhibiting periodic strategies (e.g., gizzard
shad, walleye *Sander vitreus*, 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).

Fragmentation from dams may also limit the longitudinal dispersal of fishes. Several species exhibited truncated spatial distributions below the most downstream dams in the Iowa and Cedar rivers. Of the fifteen species with truncated distributions in our study, nine also had truncated distributions in three other Iowa rivers (Pierce et al., In Press). Historical records of fish distributions described ‘large river’ species (e.g., mooneye Hiodon tergisus, shortnose gar *Lepisosteus platostomus*, and emerald shiner) as being widely distributed in both the Iowa and Cedar rivers (Loan-Wilsey et al., 2005). 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 large rivers and exhibit complex migratory behaviors (Galat and Zweimuller, 2001). These large river fishes make longitudinal movements along the main channel and (or) lateral movements among floodplain environments to access habitats that are critical to the completion of important life history events (Junk et al., 1989; Galat and Zweimuller, 2001). The construction of dams has restricted the longitudinal movements of many large 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 the longnose gar has not been observed in habitats upstream of the Cedar Rapids Milldam since
1891 (Loan-Wilsey et al., 2005). However, patterns of abundance of several large river species (e.g., shoal chub, silver chub, and shovelnose sturgeon) were positively related to mainstem fragment length and occurred in habitats upstream of these initial dams. These results indicate that the persistence of some fish species upstream of dams may be controlled by length of perennial-flowing river between dams, as suggested by Freeman et al. (2003) and Perkins and Gido (2011).

Our study provides valuable insights about the roles of landscape-scale, dam-related, and reach-scale environmental influences 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 structurally and functionally to riverine environments. The use of several fish assemblage descriptors such as taxonomy, life history strategies, tolerance traits, and habitat use guilds enabled us to connect ecological and distributional patterns with environmental variation. These diagnostic considerations are especially important in determining the proper spatial-scale of cost-effective management of fish and river ecosystems.

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Kinkead, and others at Iowa Department of Natural Resources for their guidance and support. Funding was provided by the Iowa Department of Natural Resources. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was performed under the auspices of the Institutional Animal Care and Use Committee at Iowa State University (Protocol #1-10-6850-I).
REFERENCES


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

<table>
<thead>
<tr>
<th>Variable and description</th>
<th>Abbreviation</th>
<th>Mean</th>
<th>Standard deviation</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Reach variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean annual discharge (m$^3$/s)</td>
<td>Discharge</td>
<td>2106.00</td>
<td>1520.00</td>
<td>383.00</td>
<td>5135.00</td>
</tr>
<tr>
<td>Conductivity (μS/cm)</td>
<td>Cond</td>
<td>547.00</td>
<td>55.50</td>
<td>416.00</td>
<td>648.00</td>
</tr>
<tr>
<td>Mean bank-full width (m)</td>
<td>BFW</td>
<td>97.00</td>
<td>46.30</td>
<td>43.90</td>
<td>213.20</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>Depth</td>
<td>1.29</td>
<td>0.48</td>
<td>0.61</td>
<td>2.55</td>
</tr>
<tr>
<td>Coefficient of variation of depth (%)</td>
<td>DepthCV</td>
<td>49.00</td>
<td>13.30</td>
<td>23.20</td>
<td>75.60</td>
</tr>
<tr>
<td>Mean current velocity (m/s)</td>
<td>Velocity</td>
<td>0.41</td>
<td>0.20</td>
<td>0.08</td>
<td>0.82</td>
</tr>
<tr>
<td>Coefficient of variation of current velocity (%)</td>
<td>VelocityCV</td>
<td>50.20</td>
<td>14.90</td>
<td>23.70</td>
<td>94.20</td>
</tr>
<tr>
<td>Percent coarse substrate (&lt; 2 mm)</td>
<td>Coarse</td>
<td>23.58</td>
<td>19.80</td>
<td>0.00</td>
<td>83.40</td>
</tr>
<tr>
<td>Percent overhanging canopy cover (mean % per reach)</td>
<td>Canopy</td>
<td>58.00</td>
<td>16.10</td>
<td>23.70</td>
<td>89.30</td>
</tr>
<tr>
<td>Percent of shore length rip-rap (% length of upstream shoreline)</td>
<td>RipRap</td>
<td>10.73</td>
<td>12.90</td>
<td>0.00</td>
<td>49.87</td>
</tr>
<tr>
<td>Percent of total instream cover (% of transect)</td>
<td>InstreamCover</td>
<td>18.25</td>
<td>3.50</td>
<td>9.44</td>
<td>27.22</td>
</tr>
<tr>
<td>Percent of woody debris cover (% of transect)</td>
<td>WoodCover</td>
<td>12.78</td>
<td>5.03</td>
<td>0.04</td>
<td>21.11</td>
</tr>
<tr>
<td><strong>Dam variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Distance to upstream dam (km)</td>
<td>DistUpDm</td>
<td>50.98</td>
<td>92.80</td>
<td>1.68</td>
<td>508.10</td>
</tr>
<tr>
<td>Distance to downstream dam or impoundment (km)</td>
<td>DstDnDm</td>
<td>58.02</td>
<td>63.20</td>
<td>0.01</td>
<td>198.48</td>
</tr>
<tr>
<td>Mainstem fragment length (km) between dams and impoundment boundaries</td>
<td>FragLength</td>
<td>128.23</td>
<td>122.00</td>
<td>5.52</td>
<td>510.62</td>
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<td><strong>Landscape variables</strong></td>
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<tr>
<td>Percent of urban land use area in local catchment</td>
<td>LocUrb</td>
<td>17.74</td>
<td>23.60</td>
<td>0.70</td>
<td>94.60</td>
</tr>
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<td>Percent of forested area in local catchment</td>
<td>LocFrst</td>
<td>10.04</td>
<td>15.90</td>
<td>0.00</td>
<td>69.35</td>
</tr>
<tr>
<td>Percent of wetland area in local catchment</td>
<td>LocWet</td>
<td>22.00</td>
<td>23.80</td>
<td>0.26</td>
<td>77.90</td>
</tr>
<tr>
<td>Percent of urban land use area in entire upstream catchment</td>
<td>BasinUrb</td>
<td>8.05</td>
<td>0.71</td>
<td>6.84</td>
<td>9.27</td>
</tr>
<tr>
<td>Percent of agricultural land use area in entire upstream catchment</td>
<td>BasinAg</td>
<td>82.40</td>
<td>2.40</td>
<td>78.30</td>
<td>87.20</td>
</tr>
</tbody>
</table>
Table II. Summary of percent occurrence and mean (SD) catch rates for fish species sampled in the Iowa and Cedar rivers, Iowa, during 2010 and 2011. Catch per unit effort was calculated as the number of fish per hour for electrofishing and number of fish per 50 m of trawling. Bold values indicate species occurrence and abundances truncated by downstream dams. Truncated species distributions are defined as species only occurring downstream of lowermost dams.

<table>
<thead>
<tr>
<th>Family and Species</th>
<th>Scientific Name</th>
<th>Abbreviation</th>
<th>Iowa River ($n = 15$)</th>
<th>Cedar River ($n = 18$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Percent</td>
<td>Electrofishing</td>
</tr>
<tr>
<td>Acipenseridae</td>
<td></td>
<td></td>
<td>20</td>
<td>0.83(0.06)</td>
</tr>
<tr>
<td>Lepisosteidae</td>
<td></td>
<td></td>
<td>13</td>
<td>0.26(0.75)</td>
</tr>
<tr>
<td>Longnose gar*</td>
<td>Lepisosteus osseus</td>
<td>lngr</td>
<td>20</td>
<td>2.86(6.35)</td>
</tr>
<tr>
<td>Shortnose gar</td>
<td>Lepisosteus platostomus</td>
<td>sngr</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
<td>Amiidae</td>
<td>Bowfin*</td>
<td>bwfn</td>
<td>8</td>
<td>0.08(0.29)</td>
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<td>Hiomidae</td>
<td>Goldeye*</td>
<td>gdey</td>
<td>7</td>
<td>0.11(0.44)</td>
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<td>Clupeidae</td>
<td>Mooney</td>
<td>mney</td>
<td>100</td>
<td>67.56(77.45)</td>
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<td>Cyprinidae</td>
<td>Gizzard shad</td>
<td>gcsd</td>
<td>13</td>
<td>1.02(2.98)</td>
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<td>Central stoneroller</td>
<td>Campostoma anomalum</td>
<td>cnsr</td>
<td>27</td>
<td>3.96(9.59)</td>
</tr>
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<td>Goldfish</td>
<td>Carassius auratus</td>
<td>gdfr</td>
<td>20</td>
<td>0.15(0.39)</td>
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<td>White amur</td>
<td>Ctenopharyngodon idella</td>
<td>gscp</td>
<td>67</td>
<td>0.31(0.60)</td>
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<tr>
<td>Pocket shiner</td>
<td>Cyprinella spiloptera</td>
<td>sfm</td>
<td>100</td>
<td>33.32(10.60)</td>
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<tr>
<td>Common carp*</td>
<td>Cyprinus carpio</td>
<td>cmp</td>
<td>0</td>
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</tr>
<tr>
<td>Gravel chub</td>
<td>Erinymys spincatus</td>
<td>gcb</td>
<td>0</td>
<td>1.35(3.01)</td>
</tr>
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<td>Mississippi silvery minnow*</td>
<td>Hybognathus leucisus</td>
<td>svnm</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
<td>Common shiner</td>
<td>Luciostus carinas</td>
<td>cnsr</td>
<td>27</td>
<td>3.96(9.59)</td>
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<td>Shoal chub</td>
<td>Lepidotriphus hystoma</td>
<td>skcb</td>
<td>100</td>
<td>33.32(10.60)</td>
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<tr>
<td>Silver chub</td>
<td>Macrhybopsis robberi</td>
<td>svcb</td>
<td>67</td>
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<tr>
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</tr>
<tr>
<td>Emerald shiner</td>
<td>Notemigonus crysoleucus</td>
<td>gcm</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
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<td>gcm</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
<td>Bigmouth shiner</td>
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<td>—</td>
</tr>
<tr>
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<td>—</td>
</tr>
<tr>
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<td>—</td>
</tr>
<tr>
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<td>—</td>
</tr>
<tr>
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<td>0</td>
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<td>Phenacius mirabilis</td>
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<td>Phoxinus erythrogaster</td>
<td>sbzd</td>
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</tr>
<tr>
<td>Bluntnose minnow</td>
<td>Pimelodus notatus</td>
<td>pnm</td>
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<td>1.20(1.61)</td>
</tr>
<tr>
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<td>0.38(0.71)</td>
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<tr>
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<td>bdac</td>
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TABLE II. Continued (see page 89 for heading)

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<th>Gasterosteidae</th>
<th>Esocidae</th>
<th>Ictaluridae</th>
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<th>Gasterosteidae</th>
<th>Esocidae</th>
<th>Ictaluridae</th>
<th>Catostomidae</th>
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<td>Common Name</td>
<td>Scientific Name</td>
<td>Abbreviation</td>
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<td>Other States</td>
<td>Maine</td>
<td>Vermont</td>
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<tr>
<td>Black crappie</td>
<td>Pomoxis nigromaculatus</td>
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<td>47</td>
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<td>Percidae</td>
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<tr>
<td>Western sand darter*</td>
<td>Ammocrypta clara</td>
<td>wsdr</td>
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<td>—</td>
<td>0.00(0.01)</td>
<td>50</td>
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<tr>
<td>Mud darter*</td>
<td>Etheostoma asprigene</td>
<td>msdr</td>
<td>27</td>
<td>—</td>
<td>0.01(0.02)</td>
<td>0</td>
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<tr>
<td>Rainbow darter</td>
<td>Etheostoma caeruleum</td>
<td>rbdr</td>
<td>0</td>
<td>—</td>
<td>—</td>
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<tr>
<td>Iowa darter*</td>
<td>Etheostoma exile</td>
<td>iodr</td>
<td>13</td>
<td>—</td>
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<tr>
<td>Fantail darter</td>
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<td>ftddr</td>
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<tr>
<td>Johnny darter</td>
<td>Etheostoma nigrum</td>
<td>jyddr</td>
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<tr>
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<td>Etheostoma zonale</td>
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<td>0.14(0.54)</td>
<td>0.16(0.63)</td>
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<tr>
<td>Yellow perch</td>
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<tr>
<td>Logperch*</td>
<td>Percina Caprodes</td>
<td>lgpd</td>
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<td>—</td>
<td>67</td>
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<tr>
<td>Blackside darter*</td>
<td>Percina maculata</td>
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<td>47</td>
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<td>0.48(0.82)</td>
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<tr>
<td>Skenderhead darter*</td>
<td>Percina phoxocephala</td>
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<td>0.06(0.22)</td>
<td>0.50(1.27)</td>
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<tr>
<td>Sauger</td>
<td>Sander canadensis</td>
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<td>0.08(0.29)</td>
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<td>6</td>
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<td>Walleye</td>
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<td>Sciaenidae</td>
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<tr>
<td>Freshwater drum</td>
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<td>40</td>
<td>0.61(1.09)</td>
<td>0.02(0.06)</td>
<td>44</td>
</tr>
</tbody>
</table>

* Species of greatest conservation need

# Non-native

H Hybrid
TABLE III. Species distributions truncated by dams in the Iowa and Cedar rivers, Iowa. 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 in each with an X in each river system.

<table>
<thead>
<tr>
<th>Species common name</th>
<th>Iowa River</th>
<th>Cedar River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shovelnose sturgeon $^s$</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Longnose gar $^s$</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Shortnose gar</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Bowfin $^s$</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Goldeye $^s$</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Mooneye</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Mississippi silvery minnow $^s$</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Shoal chub $^s$</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Silver chub</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Emerald shiner</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>River shiner</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Mimic shiner</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Channel shiner</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Blue sucker $^s$</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Western sand darter $^s$</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Sauger</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

$^s$ Species of greatest conservation need
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.
FIGURE 2. Species richness and percent 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.
FIGURE 3. Canonical correspondence analyses (CCA) describing patterns of fish assemblage structure using species relative abundance (CPUE) from electrofishing and trawling samples taken from 33 reaches in the Cedar and Iowa rivers, Iowa, during 2010 and 2011. Total variance explained by in axes in parentheses next to corresponding ordination axes. Habitat abbreviations are provided in Table I and fish species abbreviations are available in TABLE II.
FIGURE 4. Canonical correspondence analyses (CCAs) describing patterns of fish assemblage structure using tolerance trait, life history strategy, and habitat use guild relative abundance (CPUE) from electrofishing and trawling samples taken from 33 reaches in the Cedar and Iowa rivers, Iowa, during 2010 and 2011. Total variance explained by in axes in parentheses next to corresponding ordination axes. Habitat abbreviations are provided in TABLE I.
FIGURE 5. Canonical correspondence analyses (CCAs) describing patterns of fish assemblage structure described through percent 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 in axes in parentheses next to corresponding ordination axes. Habitat abbreviations are provided in TABLE I.
Figure 6. Percentages of explained variance in fish assemblage structure described in 11 CCA 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.
CHAPTER 4. GENERAL CONCLUSIONS

Since the first ichthyofaunal surveys conducted in the late 1800s, fish assemblage structure has noticeably changed in large river systems across Iowa. Temporal shifts in fish assemblage structure occurred in all river systems, but the magnitude of changes varied by river and spatial position in a system. The Des Moines, Iowa, and Cedar rivers exhibited significant temporal changes in species composition, primarily due to the dynamic nature of species declines and (or) expansions in distribution. Although some temporal change in species composition was observed in the Wapsipinicon River, changes were minor relative to the other systems. All study rivers, except the Maquoketa, have exhibited the majority of their compositional change in their downstream reaches. Unfortunately, little is understood about the temporal dynamics of fish assemblages in the Maquoketa River since over 50% of its species have unknown historic distributions. By using temporal trends developed for the distribution of 126 species, new conservation strategies can be developed and evaluated for fish assemblages, as well as individual fish species.

Anthropogenic disturbances (e.g., land use practices and water development) over the past 150 years have been linked to the degradation of lotic habitats and may be responsible for the declines of many fish species in Iowa. For many reasons (e.g., data paucity, sampling frequency, gear bias), the associations between the environment and the decline of riverine fish species will never be fully understood. Fortunately, using habitat-use, reproductive, and trophic guilds helped to identify prominent patterns among species exhibiting increases or declines in their distributions, which may allow inference about habitat loss and degradation. Specifically, the widespread declines of backwater dependents and fluvial specialists
suggested loss of critical off-channel and free-flowing habitats. The majority of declining backwater species also exhibited phytophilic spawning strategies, suggesting that declines may also correspond to a decrease in macrophyte abundance over time. The inferred patterns among species traits may provide valuable insight into identifying, protecting, and (or) rehabilitating critical habitat that can be capable of supporting diverse fish assemblages. Relationships between the environment and recently assessed fish assemblage structure in the Cedar and Iowa rivers provided further indication about the roles natural habitats and anthropogenic disturbance. In the Cedar and Iowa rivers, fish assemblages were primarily influenced by local-scale habitat. Among local-scale factors, discharge consistently corresponded to taxonomic and functional (e.g., life history strategy) patterns describing the organization of fish assemblages. Additional patterns of temporal flow variability have strengthened these discharge associations and suggest that fish life history strategies follow a gradient of environmental stability. However, it is still unknown how other measures of flow regime (e.g., frequency, predictability) are associated with fish assemblages and how that might reflect hydrologic alteration. An altered flow regime may reflect disturbance patterns from dams and agriculture, which were associated with multiple measures of fish assemblage structure. Further research is warranted on the influence of flow regime on fish assemblages in Iowa’s rivers. Additionally, this is the first study to comprehensively evaluate how dams influence fish assemblages in the Cedar and Iowa rivers. Thus far, dams have acted as a barrier to fish movement for several large-river species, and appear to be related to other ecological disruptions associated with fish assemblage structure. These results suggest that dams need to be considered as a source of environmental variation when conducting applied studies on fish assemblages, such as bioassessments that attempt to measure ecological
integrity. Most importantly, multi-scale environmental characters should be considered when studying environmental relationships with fish assemblages.
## APPENDIX. FUNCTIONAL AND ECOLOGICAL TRAITS OF 126 FISH SPECIES USED TO DESCRIBE HISTORIC AND RECENT PATTERNS IN FISH ASSEMBLAGE STRUCTURE IN IOWA’S NONWADEABLE RIVERS.

**SEE FOOTNOTES.**

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<tr>
<th>Family and Species</th>
<th>Scientific</th>
<th>Trophic guild 1</th>
<th>Reproductive guild 2</th>
<th>Habitat-use guild 3</th>
<th>Backwater dependence 4</th>
<th>Tolerance 5</th>
<th>Life history strategy 6</th>
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<td>Lithophil</td>
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<td>Periodic</td>
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<td>Moderate</td>
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<td>X</td>
<td>Moderate</td>
<td>Periodic-equilibrium</td>
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<td>Lithopelagophil</td>
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<td>Intolerant</td>
<td>Periodic-equilibrium</td>
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<td>Invertivore</td>
<td>Lithopelagophil</td>
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<td>Periodic</td>
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<td><em>Anguilla rostrata</em></td>
<td>Carnivore</td>
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<td>Carnivore</td>
<td>Phytophil</td>
<td>FD</td>
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<td><em>Campostoma anomalum</em></td>
<td>Herbivore-detrivore</td>
<td>Lithophil</td>
<td>FS</td>
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**Catostomidae**

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</tr>
<tr>
<td>Gasterosteidae</td>
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<tr>
<td>Brook stickleback</td>
<td>Culaea inconstans</td>
<td>Invertivore</td>
<td>Ariadnophil</td>
<td>MG</td>
<td>X</td>
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<tr>
<td>Moronidae</td>
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<tr>
<td>White bass</td>
<td>Morone chrysops</td>
<td>Carnivore</td>
<td>Phytolithophi</td>
<td>FD</td>
<td>—</td>
<td>Moderate</td>
</tr>
<tr>
<td>Yellow bass</td>
<td>Morone mississippiensis</td>
<td>Carnivore</td>
<td>Phytolithophi</td>
<td>FD</td>
<td>X</td>
<td>Moderate</td>
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<tr>
<td>Centrarchidae</td>
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<tr>
<td>Northern rock bass</td>
<td>Ambloplites rupestris</td>
<td>Carnivore</td>
<td>Polyphil</td>
<td>MG</td>
<td>—</td>
<td>Intolerant</td>
</tr>
<tr>
<td>Warmouth</td>
<td>Chaenobryttus galorus</td>
<td>Carnivore</td>
<td>Lithophi</td>
<td>MG</td>
<td>X</td>
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### Appendix continued

<table>
<thead>
<tr>
<th>Species</th>
<th>Trophic guild</th>
<th>Reproductive guild</th>
<th>Habitat-use guild</th>
<th>Conservation Status</th>
</tr>
</thead>
</table>
| **Green sunfish**  
* Lepomis cyanellus | Carnivore     | Polyphil           | MG                | Tolerant                  | Equilibrium               |
| **Pumpkinseed**  
* Lepomis gibbosus | Invertivore   | Polyphil           | MG                | X                         | —                          |
| **Orangespotted sunfish**  
* Lepomis humilis | Invertivore   | Lithophil          | Polyphil          | X                         | Moderate                  | Opportunistic -equilibrium |
| **Bluegill**  
* Lepomis macrochirus | Invertivore   | Lithophil          | Polyphil          | X                         | Moderate                  | Equilibrium               |
| **Longear sunfish**  
* Lepomis megalotis | Invertivore   | Polyphil           | Polyphil          | X                         | —                         |                        |
| **Redear sunfish**  
* Lepomis microphalus | Invertivore   | Polyphil           | MG                | X                         | —                         |                        |
| **Smallmouth bass**  
* Micropterus dolomieu | Carnivore     | Polyphil           | MG                | —                         | Intolerant                | Equilibrium               |
| **Spotted bass**  
* Micropterus punctulatus | Carnivore     | Polyphil           | MG                | —                         | —                         |                        |
| **Largemouth bass**  
* Micropterus salmoides | Carnivore     | Polyphil           | MG                | —                         | Moderate                  | Equilibrium               |
| **White crappie**  
* Pomoxis annularis | Carnivore     | Phytophil          | MG                | X                         | Moderate                  | Periodic -equilibrium     |
| **Black crappie**  
* Pomoxis nigromaculatus | Carnivore     | Phytophil          | MG                | X                         | Moderate                  | Equilibrium               |
| **Percidae**  
Western sand darter*  
* Ammocrypta clara | Benthic        | Psammophil         | FS                | —                         | Intolerant                | Opportunistic             |
| Mud darter*  
* Etheostoma asprigene | Benthic        | Phytophil          | FD                | X                         | Moderate                  | Opportunistic             |
| Rainbow darter  
* Etheostoma caeruleum | Benthic        | Lithophil          | FS                | —                         | Intolerant                | Opportunistic             |
| Bluntnose darter*  
* Etheostoma chlorosomum | Benthic        | Phytophil          | FD                | X                         | —                         |                        |
| Iowa darter*  
* Etheostoma exile | Benthic        | Phytophil          | FD                | X                         | Intolerant                | Opportunistic             |
| Fantail darter  
* Etheostoma flabellare | Benthic        | Speleophil         | FS                | —                         | Moderate                  | Opportunistic             |
| Least darter*  
* Etheostoma microperca | Benthic        | Phytophil          | MG                | X                         | —                         |                        |
| Johnny darter  
* Etheostoma nigrum | Benthic        | Speleophil         | MG                | —                         | Moderate                  | Opportunistic             |
| Orangethroat darter*  
* Etheostoma spectabile | Benthic        | Lithophil          | FS                | —                         | —                         |                        |
| Banded darter*  
* Etheostoma zonale | Benthic        | Phytophil          | FS                | —                         | Intolerant                | Opportunistic             |
| Yellow perch  
* Perca flavescens | Carnivore     | Phytophilophil     | MG                | X                         | Moderate                  | Periodic -equilibrium     |
| Northern logperch*  
* Percina caprodes | Benthic        | Lithophil          | MG                | —                         | Intolerant                | Opportunistic             |
| Gilt darter*  
* Percina evides | Benthic        | Lithophil          | FS                | —                         | —                         |                        |
| Blackside darter*  
* Percina maculata | Benthic        | Lithophil          | FS                | —                         | Moderate                  | Opportunistic -equilibrium |
| Slenderhead darter*  
* Percina phoxocephala | Benthic        | Lithophil          | FS                | —                         | Intolerant                | Opportunistic             |
| River darter*  
* Percina shumardi | Benthic        | Lithophil          | FS                | —                         | —                         |                        |
| Sauger  
* Stizostedion canadense | Carnivore     | Lithopelagophil    | MG                | —                         | Moderate                  | Periodic -equilibrium     |
| Walleye  
* Stizostedion vitreum | Carnivore     | Lithopelagophil    | MG                | —                         | Moderate                  | Periodic                 |
| **Sciaenidae**  
Freshwater drum  
* Aplodinotus grunniens | Benthic        | Pelagophil         | MG                | —                         | Moderate                  | Periodic                 |

* Species of greatest conservation need  
E Non-native to Iowa

1 Trophic guild classifications were taken from Pflieger (1997), Lyons et al. (2001), and Wilton (2004).
2 Reproductive guild classifications were taken from Balon (1978).
3 Habitat-use guild abbreviations: FD – fluvial dependent, FS – fluvial specialist, and MG – macrohabitat generalist; were taken from Kinsolving and Bain (1993) and Galat and Zweimüller (2001).
Backwater associations and dependence determined by using Schramm (2004), Goldstein and Meador (2005), and Gutreuter et al. (2009).

Classifications of fish tolerances to environmental degradation were taken from Wilton (2004).

Life history strategies were classified based off of the Winemiller and Rose (1992) life history model and fish life history strategies were determined using a modification of the “soft classification” approach (Olden and Kennard 2010) where life histories were determined objectively for each species using life history data from the Midwest from Carlander (1969,1977,1997). Although all data was gathered for 126 species, life history strategies were primarily determined for the 85 species analyzed in Chapter 3.