Am. Midl. Nat. (2014) 171:27–53

Historical Changes in Fish Assemblage Structure in Midwestern Nonwadeable Rivers

TIMOTHY P. PARKS[1]
Department of Natural Resource Ecology and Management, Iowa State University, Ames 50011

MICHAEL C. QUIST
U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Resources, University of Idaho, Moscow 83844

AND

CLAY L. PIERCE
U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Iowa State University, Ames 50011

Abstract.—Historical 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 historical 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. Spatiotemporal shifts in species composition were analyzed at the river and river section scale using cluster analysis, pairwise Jaccard's dissimilarities, 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 Moines, Cedar, and Iowa rivers within the historical and recent 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.*, 2008). The successful conservation of lotic fish fauna is dependent upon an adequate understanding of how fish faunas change through time and space (Matthews, 1998; Jackson *et al.*, 2001). In the last 10 y, 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 y, large rivers have been increasingly subjected to the cumulative effects of anthropogenic disturbances such as point-source pollution, urbanization, agriculture, channel modification, impoundment, and nonnative species introductions (Sparks, 1995; Hughes *et al.*, 2005). These human disturbances have directly

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[1] Corresponding author present address: Wisconsin Department of Natural Resources, 810 W. Maple Street, Spooner, WI 54801; email: tpark765@gmail.com or Timothy.Parks@wisconsin.gov

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.*,1986; 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 fishes (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.*, 2013), 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 historical 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 historical 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 that have 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 that 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 y, 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 nonindigenous species from various stocking practices have also led to negative consequences for native ichthyofauna in Iowa (Bernstein and Olson, 2001).

The purpose of this study was to investigate changes in the historical ichthyofauna of five nonwadeable rivers in Iowa. This was accomplished by evaluating long-term trends in the spatial distributions of resident fish species. We also assessed and compared historical 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 nonindigenous species (*e.g.,* stocking practices), we expected fish faunas to become more taxonomically similar over time.

METHODS

STUDY AREA

Historical 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 coordinates for the mouth of each river are: 40.38003N, −91.42204W (Des Moines), 41.16005N, −91.02379W (Iowa), 41.72943N, −90.31946W (Cedar), 41.72943N, −90.31946W (Wapsipinicon River), and 42.18872N, −90.30899W (Maquoketa River). The rivers flow northwest to southeast and drain areas varying from 4808 to 37,141 km^2 (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 y; 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). According to recent research by Falcone *et al.* (2010), 75–80% of the original land cover has been transformed for agricultural land use (*i.e.*, row crop and pasture) and 6–9% of the land cover was transformed for urban land use among basins (Table 1). 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 >6150 ML(mega liter) per km^2 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/km^2 across river basins (Falcone *et al.*, 2010). Since 1970, the total 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 1884–2011 were gathered from a variety of sources and databases. Historical 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

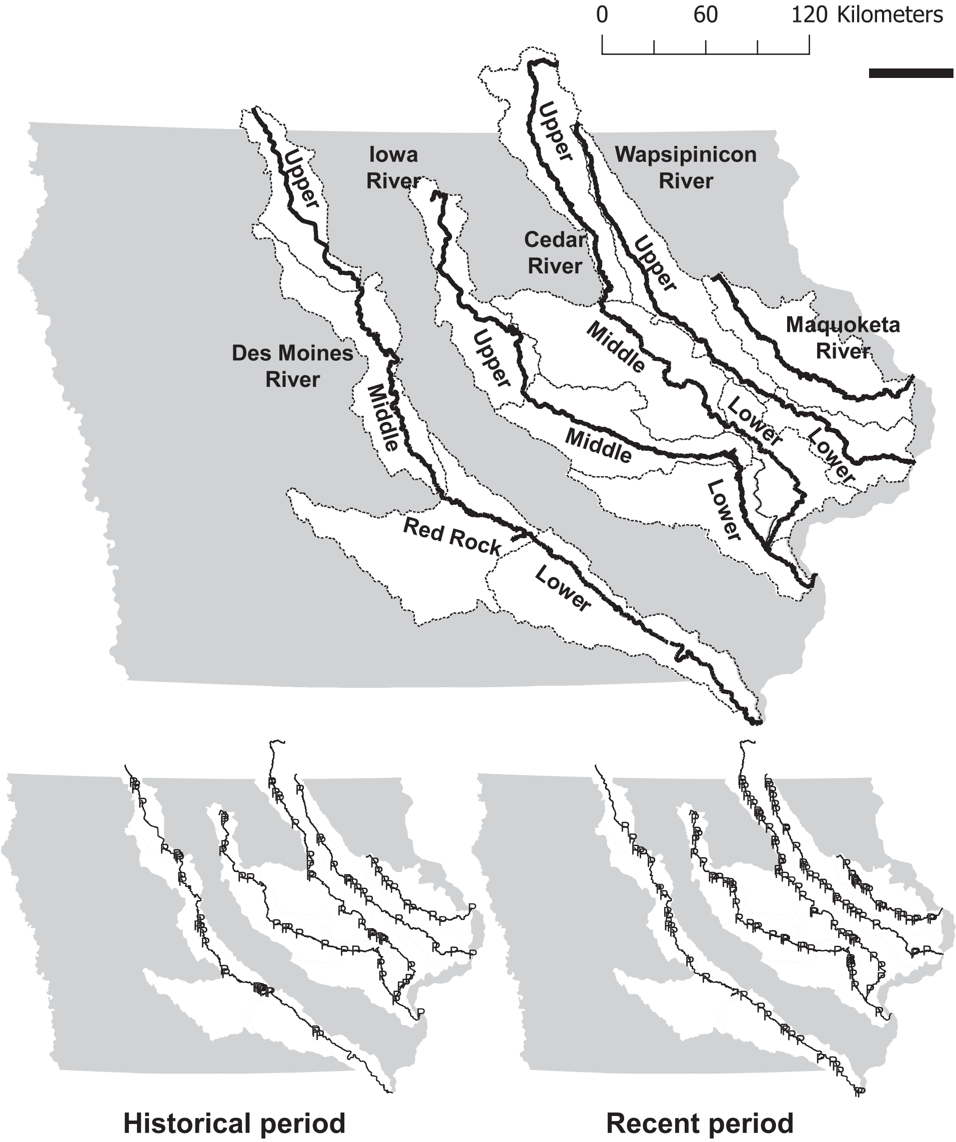

FIG. 1.—Map of the study river systems (top) in Iowa and their corresponding 8-digit hydrologic unit code basins (HUC-8): Upper, Middle, Red Rock (Lake), and Lower. The lower panel illustrates the spatial distribution of mainstem sampling sites in the Des Moines, Iowa, Cedar, Wapsipinicon, and Maquoketa rivers, during the historical (1884–1969) and recent (1990–2011) assessment periods

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,

TABLE 1.—Basin, riparian, and mainstem anthropogenic impacts characterized through land use and instream development in five nonwadeable river drainages in Iowa, according to Falcone *et al.* (2010)

		Land use				Instream development			
		Basin		Riparian		Mainstem		Basin	
River	Drainage (km^2)	Urban (%)	Agriculture (%)	Urban (%)	Agriculture (%)	Modified channel length (%)	No. dams	Change in dam storage (mega liters)	Change in no. dams
Maquoketa River	4808.6	6.0	75.3	7.1	40.6	18.9	7	1.5	8
Wapsipinicon River	6479.6	7.4	80.5	6.5	42.5	35.3	10	0.8	4
Cedar River	20,050.5	9.1	80.4	10.6	34.2	65.9	9	3.4	45
Iowa River	32,429.9	8.5	79.3	9.7	20.3	49.7	8	53.4	80
Des Moines River	37,141.9	7.1	78.9	8.7	44.6	64.5	10	94.5	459

Redlands, CA). Only mainstem nonwadeable river samples were considered for our analyses; no major tributaries were included. Our analyses were 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

Historical changes in fish distributions were described by comparing species occurrences from historical 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.*, large changes in land use). We defined the historical time period as 1884–1969 (Fig. 1; lower, left panel). This time period included 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 historical 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 statewide land use changes had stabilized by this time period (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 historical 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 locations (*n*) was iteratively sampled in each river to estimate species occurrences. Resampling was performed 1000 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 historical period to create a distribution of differences. Differences in percent occurrence iterations were calculated between assessment period iterations (*i.e.*, 1000 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 historical change. Conversely, if confidence intervals exhibited only positive differences or negative differences, then a species has either declined or increased in distribution, respectively. Unknown trends in species distributions were defined as those in which a species was detected less than three times in historical samples. Only nonnative species introductions were exempt from this unknown trend determination.

Historical 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 nondegraded 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).

Spatiotemporal 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 historical 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 approximately 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 patterns of species turnover were directly 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.*, historical 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.*, 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.*, rivers in the UMRB) at two different time periods (*i.e.*, 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, historical 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.*, 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

Historical 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 of species declines (*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.

TABLE 2.—Estimated percent occurrence (±95% confidence interval) of fish species sampled in the Des Moines, Iowa, Cedar, Wapsipinicon, and Maquoketa rivers, during the historical (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

		Cedar		Des Moines		Iowa		Maquoketa		Wapsipinicon	
Family and species	Scientific name	H (n = 24)	R (n = 34)	H (n = 34)	R (n = 28)	H (n = 16)	R (n = 35)	H (n = 11)	R (n = 21)	H (n = 14)	R (n = 27)
Petromyzontidae											
Northern brook lamprey^S	*Ichthyomyzon fossor*	—	—	—	—	—	—	0(0.0)	9(1.7)	—	—
Silver lamprey^S	*Ichthyomyzon unicuspis*	—	—	3(0.6)	0(0.0)	—	—	0(0.0)	5(1.2)	—	—
American brook lamprey^S	*Lampetra appendix*	0(0.0)	3(0.6)	—	—	0(0.0)	3(0.6)	0(0.0)	14(2)	0(0.0)	22(1.7)
Acipenseridae											
Shovelnose sturgeon^S	*Scaphirhynchus platorynchus*	4(1.1)	27(1.5)	0(0.0)	7(1.0)	0(0.0)	12(1.0)	0(0.0)	19(2.2)	0(0.0)	4(0.8)
Polydontidae											
Paddlefish^S	*Polyodon spathula*	4(1.0)	3(0.6)	3(0.6)	4(0.7)	6(1.8)	6(0.8)	—	—	—	—
Lepisosteidae											
Spotted gar	*Lepisosteus oculatus*	—	—	0(0)	7(1.0)	—	—	—	—	—	—
Longnose gar^S	*Lepisosteus osseus*	4(1.1)	18(1.4)	12(1.1)	14(1.4)	6(1.8)	9(0.9)	0(0.0)	14(2.0)	7(2.4)	4(0.7)
Shortnose gar	*Lepisosteus platostomus*	4(1.1)	24(1.5)	3(0.6)	21(1.6)	6(1.9)	17(1.3)	0(0.0)	14(1.9)	7(2.5)	7(1.1)
Amiidae											
Bowfin^S	*Amia calva*	12(1.7)	0(0.0)	—	—	12(2.5)	6(0.8)	—	—	7(2.4)	4(0.8)
Hiodontidae											
Goldeye^S	*Hiodon alosoides*	0(0.0)	3(0.6)	27(1.6)	14(1.3)	0(0.0)	3(0.5)	—	—	—	—
Mooneye	*Hiodon tergisus*	8(1.4)	9(1.0)	0(0)	22(1.6)	0(0.0)	6(0.8)	9(3.3)	19(2.2)	0(0.0)	4(0.8)
Anguillidae											
American eel^S	*Anguilla rostrata*	12(1.7)	0(0.0)	21(1.4)	4(0.7)	6(1.8)	0(0.0)	—	—	—	—
Clupeidae											
Skipjack herring	*Alosa chrysochloris*	—	—	0(0.0)	4(0.7)	—	—	—	—	—	—
Gizzard shad	*Dorosoma cepedianum*	38(2.4)	41(1.7)	15(1.3)	47(2.0)	13(2.5)	60(1.6)	9(3.3)	14(2.0)	14(3.4)	15(1.5)

TABLE 2.—Continued

		Cedar		Des Moines		Iowa		Maquoketa		Wapsipinicon	
Family and species	Scientific name	H (n = 24)	R (n = 34)	H (n = 34)	R (n = 28)	H (n = 16)	R (n = 35)	H (n = 11)	R (n = 21)	H (n = 14)	R (n = 27)
Cyprinidae											
Central stoneroller	*Campostoma anomalum*	25(2.3)	27(1.6)	23(1.5)	4(0.7)	44(3.7)	17(1.2)	27(5.1)	52(2.8)	28(4.4)	26(1.8)
Largescale stoneroller^{S}	*Campostoma oligolepis*	—	—	—	—	0(0.0)	6(0.8)	—	—	—	—
Goldfish^{I}	*Carassius auratus*	4(1.1)	9(1.0)	—	—	0(0.0)	9(0.9)	—	—	—	—
Lake chub	*Couesius plumbeus*	—	—	—	—	6(1.9)	0(0.0)	—	—	—	—
White amur^{I}	*Ctenopharyngodon idella*	0(0.0)	9(1.0)	0(0.0)	11(1.2)	0(0.0)	20(1.3)	0(0.0)	5(1.2)	—	—
Red shiner	*Cyprinella lutrensis*	21(2.1)	6(0.8)	21(1.3)	18(1.5)	6(1.8)	6(0.8)	—	—	7(2.6)	0(0.0)
Spotfin shiner	*Cyprinella spiloptera*	29(2.4)	88(1.1)	33(1.7)	54(1.9)	25(3.1)	77(1.4)	36(5.5)	86(2.0)	43(4.8)	85(1.5)
Common carp^{I}	*Cyprinus carpio*	42(2.6)	97(0.6)	76(1.5)	82(1.5)	56(3.8)	86(1.1)	55(5.7)	95(1.2)	57(4.6)	63(2.0)
Gravel chub ^{S}	*Erimystax x-punctatus*	17(1.9)	44(1.7)	18(1.3)	0(0.0)	—	—	—	—	14(3.5)	0(0.0)
Western silvery minnow	*Hybognathus argyritis*	—	—	0(0.0)	4(0.7)	—	—	—	—	—	—
Brassy minnow	*Hybognathus hankinsoni*	8(1.4)	9(1.0)	18(1.4)	7(1.0)	19(3.0)	26(1.4)	9(3.3)	5(1.2)	29(4.4)	30(1.9)
Mississippi silvery minnow^{S}	*Hybognathus nuchalis*	13(1.7)	6(0.8)	6(0.8)	4(0.7)	19(3.0)	0(0.0)	9(3.3)	5(1.2)	28(4.4)	11(1.3)
Pallid shiner^{S}	*Hybopsis amnis*	—	—	3(0.6)	0(0.0)	—	—	—	—	—	—
Bighead carp^{I}	*Hypophthalmichthys nobilis*	—	—	0(0.0)	4(0.7)	—	—	—	—	—	—
Common shiner	*Luxilus cornutus*	38(2.5)	29(1.6)	27(1.5)	4(0.7)	25(3.1)	23(1.4)	27(5.1)	43(2.8)	43(4.8)	63(2.0)
Redfin shiner^{S}	*Lythrurus umbratilis*	4(1.0)	6(0.8)	3(0.6)	0(0.0)	0(0.0)	11(1.1)	—	—	14(3.5)	7.4(1.1)
Shoal chub	*Macrhybopsis hyostoma*	8(1.5)	12(1.1)	21(1.4)	22(1.6)	0(0.0)	3(0.6)	0(0.0)	5(1.2)	0(0.0)	4(0.8)
Silver chub	*Macrhybopsis storeriana*	8(1.5)	9(1.0)	21(1.4)	36(1.8)	25(3.2)	34(1.5)	18(4.4)	14(2.0)	14(3.4)	11(1.3)
Hornyhead chub	*Nocomis biguttatus*	29(2.4)	27(1.6)	21(1.4)	11(1.2)	19(2.8)	17(1.2)	18(4.4)	29(2.5)	21(4.0)	30(1.9)
Golden shiner	*Notemigonus crysoleucas*	25(2.3)	6(0.8)	15(1.2)	4(0.7)	12(2.5)	12(1.1)	0(0.0)	10(1.6)	36(4.9)	11(1.3)
Pugnose shiner^{S}	*Notropis anogenus*	—	—	3(0.6)	0(0.0)	—	—	—	—	—	—
Emerald shiner	*Notropis atherinoides*	13(1.6)	35(1.6)	24(1.5)	43(1.9)	13(2.4)	12(1.1)	18(4.4)	76(2.4)	14(3.5)	26(1.9)
River shiner	*Notropis blennius*	25(2.2)	18(1.3)	26(1.5)	7(1)	6(1.8)	6(0.8)	9(3.3)	10(1.6)	7(2.5)	0(0.0)
Ironcolor shiner^{S}	*Notropis chalybaeus*	4(1.0)	0(0.0)	—	—	—	—	—	—	—	—
Bigmouth shiner	*Notropis dorsalis*	42(2.6)	47(1.7)	32(1.6)	36(1.9)	44(3.8)	51(1.7)	46(5.7)	43(2.8)	57(4.8)	63(2.0)
Blackchin shiner^{S}	*Notropis heterodon*	4(1.0)	0(0.0)	3(0.6)	0(0.0)	6(1.8)	0(0.0)	—	—	—	—
Blacknose shiner^{S}	*Notropis heterolepis*	4(1.0)	0(0.0)	3(0.6)	0(0.0)	6(1.9)	0(0.0)	—	—	7(2.4)	0(0.0)
Ozark minnow^{S}	*Notropis nubilus*	0(0.0)	15(1.3)	—	—	6(1.8)	0(0.0)	0(0.0)	9(1.6)	7(2.4)	0(0.0)
Rosyface shiner	*Notropis rubellus*	8(1.5)	41(1.7)	21(1.5)	4(0.7)	12(2.5)	12(1.0)	9(3.3)	14(1.9)	21(4.1)	30(1.9)
Sand shiner	*Notropis stramineus*	50(2.6)	82(1.4)	41(1.8)	50(2.0)	31(3.5)	60(1.7)	27(5.1)	76(2.4)	43(4.8)	81(1.6)

TABLE 2.—Continued

Family and species	Scientific name	Cedar		Des Moines		Iowa		Maquoketa		Wapsipinicon	
		H (n = 24)	R (n = 34)	H (n = 34)	R (n = 28)	H (n = 16)	R (n = 35)	H (n = 11)	R (n = 21)	H (n = 14)	R (n = 27)
Weed shiner^{S}	*Notropis texanus*	4(1.0)	0(0.0)	—	—	6(1.8)	0(0.0)	—	—	—	—
Topeka shiner*	*Notropis topeka*	4(1.0)	0(0.0)	12(1.1)	0(0.0)	25(3.2)	0(0.0)	—	—	—	—
Mimic shiner	*Notropis volucellus*	0(0.0)	6(0.8)	0(0.0)	7(1.0)	0(0.0)	11(1.1)	0(0.0)	5(1.2)	0(0.0)	4(0.8)
Channel shiner	*Notropis wickliffi*	0(0.0)	3(0.6)	0(0.0)	7(1.0)	0(0.0)	9(0.9)	—	—	0(0.0)	4(0.8)
Suckermouth minnow	*Phenacobius mirabilis*	33(2.5)	21(1.3)	32(1.7)	11(1.2)	18(2.9)	23(1.4)	18(4.4)	24(2.3)	14(3.3)	15(1.5)
Southern redbelly dace^{S}	*Phoxinus erythrogaster*	0(0.0)	9(1.0)	—	—	6(1.7)	0(0.0)	27(5.1)	9(1.6)	7(2.5)	7(1.1)
Bluntnose minnow	*Pimephales notatus*	50(2.6)	74(1.6)	38(1.6)	50(2.0)	44(3.8)	54(1.6)	36(5.5)	76(2.4)	50(4.9)	78(1.7)
Fathead minnow	*Pimephales promelas*	21(2.1)	29(1.6)	35(1.7)	25(1.7)	32(3.4)	49(1.7)	9(3.3)	29(2.5)	29(4.3)	37(1.9)
Bullhead minnow	*Pimephales vigilax*	25(2.1)	77(1.5)	32(1.7)	32(1.8)	13(2.5)	23(1.4)	9(3.3)	43(2.8)	29(4.6)	48(2.1)
Blacknose dace	*Rhinichthys atratulus*	8(1.4)	9(1.0)	12(1.2)	0(0.0)	0(0.0)	11(1.1)	9(3.3)	24(2.4)	7(2.6)	7(1.1)
Longnose dace^{S}	*Rhinichthys cataractae*	—	—	0(0.0)	7(1.0)	—	—	0(0.0)	5(1.2)	—	—
Creek chub	*Semotilus atromaculatus*	29(2.3)	38(1.7)	47(1.8)	7(1.0)	19(3.0)	14(1.1)	36(5.4)	33(2.7)	14(3.4)	41(2.0)
Catostomidae											
River carpsucker	*Carpiodes carpio*	8(1.4)	82(1.3)	18(1.3)	72(1.8)	6(1.8)	54(1.7)	18(4.4)	67(2.7)	14(3.4)	48(2.0)
Quillback carpsucker	*Carpiodes cyprinus*	50(2.5)	88(1.1)	41(1.7)	53(2.0)	57(3.9)	43(1.6)	9(3.3)	76(2.3)	72(4.3)	59(2.0)
Highfin carpsucker	*Carpiodes velifer*	12(1.7)	77(1.5)	12(1.1)	14(1.3)	6(1.8)	37(1.6)	0(0.0)	48(2.7)	14(3.4)	52(2.0)
White sucker	*Catostomus commersoni*	33(2.4)	50(1.7)	71(1.6)	14(1.3)	63(3.7)	34(1.6)	9(3.3)	81(2.1)	29(4.4)	59(2.1)
Blue sucker^{S}	*Cycleptus elongatus*	0(0.0)	29(1.6)	0(0.0)	11(1.2)	0(0.0)	6(0.8)	0(0.0)	5(1.2)	—	—
Lake chubsucker	*Erimyzon succetta*	4(1.0)	0(0.0)	—	—	—	—	—	—	—	—
Northern hog sucker	*Hypentelium nigricans*	25(2.2)	65(1.6)	23(1.5)	25(1.7)	19(2.8)	26(1.4)	9(3.3)	81(2.2)	29(4.4)	70(1.9)
Smallmouth buffalo	*Ictiobus bubalus*	21(2.0)	44(1.7)	0(0.0)	57(1.9)	0(0.0)	51(1.6)	9(3.3)	14(1.9)	0(0.0)	22(1.8)
Bigmouth buffalo	*Ictiobus cyprinellus*	29(2.4)	50(1.7)	24(1.5)	32(1.9)	25(3.2)	43(1.6)	0(0.0)	33(2.7)	7(2.5)	33(2.0)
Black buffalo^{S}	*Ictiobus niger*	8(1.4)	15(1.3)	6(0.8)	4(0.7)	0(0.0)	29(1.5)	0(0.0)	10(1.6)	0(0.0)	11(1.3)
Spotted sucker^{S}	*Minytrema melanops*	—	—	—	—	6(1.9)	0(0.0)	—	—	—	—
Silver redhorse	*Moxostoma anisurum*	21(2.1)	65(1.7)	27(1.5)	18(1.5)	6(1.8)	23(1.4)	0(0.0)	24(2.4)	15(3.4)	52(2.1)
River redhorse^{S}	*Moxostoma carinatum*	0(0.0)	35(1.7)	—	—	0(0.0)	9(0.9)	0(0.0)	5(1.2)	—	—
Black redhorse^{S}	*Moxostoma duquesnei*	8(1.4)	15(1.2)	9(1.0)	0(0.0)	19(2.9)	9(0.9)	0(0.0)	24(2.3)	22(3.9)	4(0.8)
Golden redhorse	*Moxostoma erythrurum*	21(2.1)	85(1.2)	27(1.5)	47(1.9)	37(3.6)	51(1.7)	9(3.3)	95(1.2)	36(4.7)	78(1.7)
Shorthead redhorse	*Moxostoma macrolepidotum*	29(2.4)	97(0.6)	41(1.7)	46(2.0)	19(3.0)	77(1.3)	0(0.0)	76(2.4)	21(4.0)	85(1.5)

TABLE 2.—Continued

Family and species	Scientific name	Cedar		Des Moines		Iowa		Maquoketa		Wapsipinicon	
		H (n = 24)	R (n = 34)	H (n = 34)	R (n = 28)	H (n = 16)	R (n = 35)	H (n = 11)	R (n = 21)	H (n = 14)	R (n = 27)
Ictaluridae											
Black bullhead	*Ameiurus melas*	42(2.6)	3(0.6)	32(1.7)	11(1.2)	50(3.6)	26(1.4)	0(0.0)	15(1.9)	28(4.4)	26(1.8)
Yellow bullhead	*Ameiurus natalis*	13(1.7)	3(0.6)	3(0.6)	11(1.2)	6(1.8)	23(1.4)	9(3.3)	52(2.7)	7(2.6)	37(1.9)
Brown bullhead^{S}	*Ameiurus nebulosus*	4(1.1)	0(0.0)	3(0.6)	0(0.0)	—	—	—	—	—	—
Channel catfish	*Ictalurus punctatus*	42(2.6)	79(1.4)	91(1.0)	64(1.9)	50(3.7)	69(1.5)	46(5.7)	81(2.2)	43(4.8)	71(1.9)
Slender madtom^{S}	*Noturus exilis*	4(1.0)	3(0.6)	—	—	0(0.0)	3(0.6)	—	—	—	—
Stonecat	*Noturus flavus*	8(1.4)	47(1.7)	47(1.8)	18(1.5)	12(2.5)	34(1.6)	0(0.0)	43(2.8)	7(2.5)	26(1.8)
Tadpole madtom^{S}	*Noturus gyrinus*	13(1.6)	9(1.0)	18(1.3)	0(0.0)	13(2.5)	3(0.5)	—	—	—	—
Freckled madtom^{S}	*Noturus nocturnus*	0(0.0)	3(0.6)	—	—	0(0.0)	11(1.0)	—	—	—	—
Flathead catfish	*Pylodictis olivaris*	13(1.7)	41(1.8)	35(1.7)	57(2.0)	25(3.3)	51(1.7)	0(0.0)	14(1.9)	14(3.4)	15(1.5)
Esocidae											
Grass pickerel^{S}	*Esox americanus*	17(2.0)	0(0.0)	—	—	—	—	—	—	—	—
Northern pike	*Esox lucius*	21(2.1)	62(1.7)	29(1.6)	14(1.3)	38(3.6)	40(1.6)	0(0.0)	53(2.8)	50(4.9)	63(2.0)
Umbridae											
Central mudminnow^{S}	*Umbra limi*	4(1.0)	3(0.6)	—	—	6(1.8)	0(0.0)	—	—	7(2.6)	11(1.3)
Salmonidae											
Rainbow trout^{I}	*Oncorhynchus mykiss*	0(0.0)	3(0.6)	—	—	—	—	0(0.0)	19(2.2)	7(2.6)	4(0.8)
Brown trout^{I}	*Salmo trutta*	—	—	—	—	—	—	0(0.0)	14(2.0)	7(2.4)	4(0.8)
Brook trout^{S}	*Salvelinus fontinalis*	—	—	—	—	—	—	0(0.0)	5(1.3)	—	—
Fundulidae											
Banded killifish^{S}	*Fundulus diaphanus*	—	—	3(0.6)	0(0.0)	6(1.8)	0(0.0)	—	—	—	—
Starhead topminnow	*Fundulus dispar*	4(1.0)	0(0.0)	—	—	—	—	—	—	—	—
Blackstripe topminnow^{S}	*Fundulus notatus*	4(1.0)	3(0.6)	—	—	6(1.9)	0(0.0)	0(0.0)	5(1.2)	7 (2.6)	4(0.8)
Atherinopsidae											
Brook silverside	*Labidesthes sicculus*	29(2.3)	3(0.6)	3(0.6)	0(0.0)	0(0.0)	3(0.5)	9(3.3)	19(2.2)	14(3.4)	0(0.0)
Gasterosteidae											
Brook stickleback	*Culaea inconstans*	8(1.4)	0(0.0)	3(0.6)	0(0.0)	6(1.9)	9(0.9)	0(0.0)	5(1.2)	14(3.5)	11(1.3)

TABLE 2.—Continued

Family and species	Scientific name	Cedar H (n = 24)	Cedar R (n = 34)	Des Moines H (n = 34)	Des Moines R (n = 28)	Iowa H (n = 16)	Iowa R (n = 35)	Maquoketa H (n = 11)	Maquoketa R (n = 21)	Wapsipinicon H (n = 14)	Wapsipinicon R (n = 27)
Moronidae											
White bass	*Morone chrysops*	8(1.4)	32(1.6)	3(0.6)	50(2.0)	12(2.6)	43(1.7)	18(4.4)	33(2.6)	14(3.4)	7(1.1)
Yellow bass	*Morone mississippiensis*	4(1.0)	9(1.0)	6(0.8)	0(0.0)	—	—	0(0.0)	19(2.2)	—	—
Centrarchidae											
Northern rock bass	*Ambloplites rupestris*	25(2.2)	41(1.8)	18(1.4)	4(0.7)	0(0.0)	9(0.9)	0(0.0)	62(2.7)	14(3.4)	48(2.0)
Warmouth	*Chaenobryttus gulosus*	20(2.1)	0(0.0)	—	—	6(1.8)	0(0.0)	—	—	—	—
Green sunfish	*Lepomis cyanellus*	50(2.4)	71(1.6)	68(1.7)	39(1.8)	50(3.8)	60(1.6)	0(0.0)	57(2.8)	50(4.8)	85(1.5)
Pumpkinseed	*Lepomis gibbosus*	8(1.5)	3(0.6)	—	—	—	—	—	—	7(2.5)	4(0.8)
Orangespotted sunfish	*Lepomis humilis*	33(2.4)	35(1.7)	39(1.7)	14(1.3)	31(3.5)	37(1.6)	9(3.3)	5(1.2)	57(4.8)	41(2.1)
Bluegill	*Lepomis macrochirus*	50(2.6)	50(1.7)	44(1.8)	61(1.9)	32(3.4)	60(1.6)	37(5.5)	86(1.9)	50(4.7)	48(2.0)
Longear sunfish	*Lepomis megalotis*	4(1.1)	0(0.0)	3(0.6)	0(0.0)	6(1.8)	0(0.0)	—	—	—	—
Redear sunfish^{I}	*Lepomis microlophus*	—	—	0(0.0)	4(0.7)	—	—	—	—	—	—
Smallmouth bass	*Micropterus dolomieu*	38(2.6)	97(0.6)	50(1.7)	39(1.9)	31(3.4)	54(1.6)	18(4.5)	95(1.2)	43(4.9)	70(1.9)
Spotted bass^{I}	*Micropterus punctulatus*	—	—	—	—	0(0.0)	3(0.5)	—	—	—	—
Largemouth bass	*Micropterus salmoides*	38(2.5)	35(1.6)	35(1.7)	39(1.9)	19(2.9)	37(1.6)	36(5.5)	57(2.8)	43(4.8)	67(1.9)
White crappie	*Pomoxis annularis*	25(2.2)	15(1.3)	41(1.7)	18(1.4)	37(3.7)	23(1.4)	36(5.5)	9(1.7)	22(3.8)	26(1.9)
Black crappie	*Pomoxis nigromaculatus*	42(2.5)	44(1.8)	30(1.6)	32(1.8)	25(3.2)	34(1.6)	9(3.3)	53(2.9)	50(4.9)	56(2.1)
Percidae											
Western sand darter^{S}	*Ammocrypta clara*	8(1.4)	29(1.5)	21(1.4)	0(0.0)	0(0.0)	3(0.6)	—	—	15(3.3)	4(0.8)
Mud darter^{S}	*Etheostoma asprigene*	8(1.4)	0(0.0)	0(0.0)	4(0.7)	0(0.0)	11(1.1)	—	—	—	—
Rainbow darter	*Etheostoma caeruleum*	13(1.7)	12(1.2)	—	—	—	—	18(4.4)	24(2.4)	7(2.4)	4(0.8)
Bluntnose darter^{S}	*Etheostoma chlorosomum*	4(1.0)	0(0.0)	—	—	—	—	—	—	7(2.6)	0(0.0)
Iowa darter^{S}	*Etheostoma exile*	4(1.0)	0(0.0)	9(1.0)	4(0.7)	19(3.0)	6(0.8)	0(0.0)	5(1.2)	7(2.5)	15(1.4)
Fantail darter	*Etheostoma flabellare*	13(1.7)	24(1.5)	15(1.2)	14(1.4)	19(2.9)	14(1.2)	0(0.0)	24(2.4)	14(3.5)	26(1.8)
Least darter^{S}	*Etheostoma microperca*	4(1.0)	0(0.0)	—	—	—	—	—	—	—	—
Johnny darter	*Etheostoma nigrum*	42(2.5)	64(1.7)	26(1.6)	11(1.2)	44(3.6)	57(1.7)	0(0.0)	52(2.8)	50(4.9)	67(1.9)
Orangethroat darter^{S}	*Etheostoma spectabile*	—	—	0(0.0)	4(0.7)	—	—	—	—	—	—
Banded darter^{S}	*Etheostoma zonale*	12(1.7)	44(1.7)	21(1.4)	11(1.2)	0(0.0)	9(0.9)	9(3.3)	53(2.8)	7(2.5)	33(1.9)

TABLE 2.—Continued

Family and species	Scientific name	Cedar		Des Moines		Iowa		Maquoketa		Wapsipinicon	
		H (n = 24)	R (n = 34)	H (n = 34)	R (n = 28)	H (n = 16)	R (n = 35)	H (n = 11)	R (n = 21)	H (n = 14)	R (n = 27)
Yellow perch	*Perca flavescens*	4(1.0)	15(1.2)	18(1.4)	7(1.0)	6(1.8)	3(0.6)	—	—	—	—
Northern logperch[S]	*Percina caprodes*	8(1.4)	56(1.7)	12(1.1)	0(0.0)	0(0.0)	3(0.6)	—	—	—	—
Gilt darter[S]	*Percina evides*	4(1.1)	0(0.0)	3(0.6)	0(0.0)	—	—	—	—	—	—
Blackside darter[S]	*Percina maculata*	13(1.7)	24(1.5)	30(1.5)	0(0.0)	19(2.9)	37(1.6)	0(0.0)	19(2.2)	22(3.8)	41(2.0)
Slenderhead darter[S]	*Percina phoxocephala*	12(1.7)	74(1.6)	18(1.4)	14(1.4)	0(0.0)	43(1.6)	0(0.0)	29(2.4)	14(3.4)	15(1.5)
River darter[S]	*Percina shumardi*	—	—	—	—	0(0.0)	3(0.6)	—	—	7(2.4)	4(0.8)
Sauger	*Stizostedion canadense*	8(1.5)	15(1.3)	3(0.6)	7(1.0)	0(0.0)	9(1.0)	0(0.0)	19(2.1)	0(0.0)	11(1.3)
Walleye	*Stizostedion vitreum*	21(2.0)	77(1.5)	59(1.7)	50(1.9)	13(2.4)	51(1.7)	18(4.4)	86(1.9)	22(4.1)	52(2.0)
Sciaenidae											
Freshwater drum	*Aplodinotus grunniens*	8(1.4)	41(1.7)	27(1.6)	64(1.8)	12(2.5)	23(1.4)	9(3.3)	14(1.9)	7(2.6)	15(1.5)

[S] Species of greatest conservation need

[I] Nonnative to Iowa

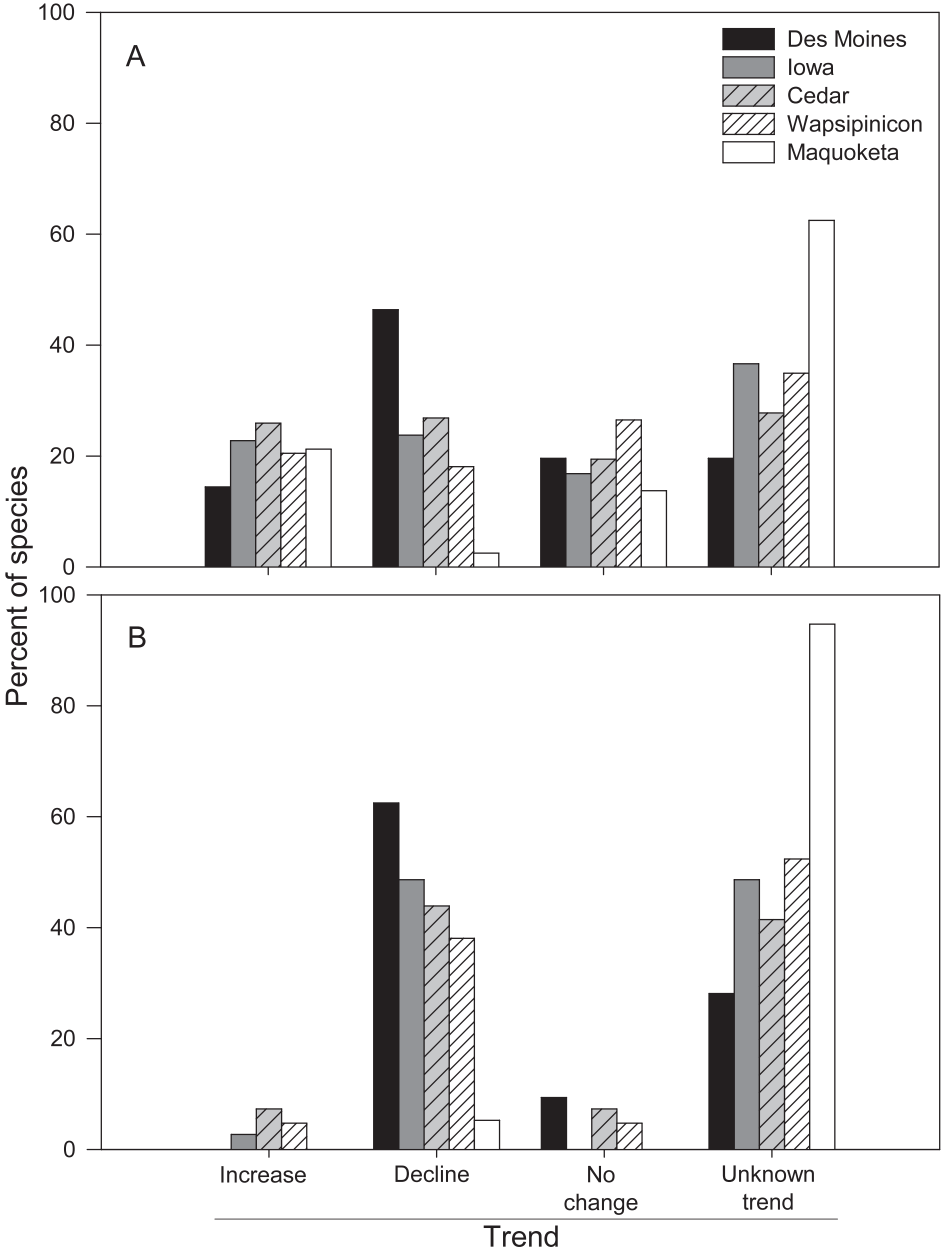

FIG. 2.—Percentage of all species (**A**) and species of greatest conservation need (**B**) exhibiting temporal trends in occurrence in the Des Moines, Iowa, Cedar, Wapsipinicon, and Maquoketa rivers of Iowa

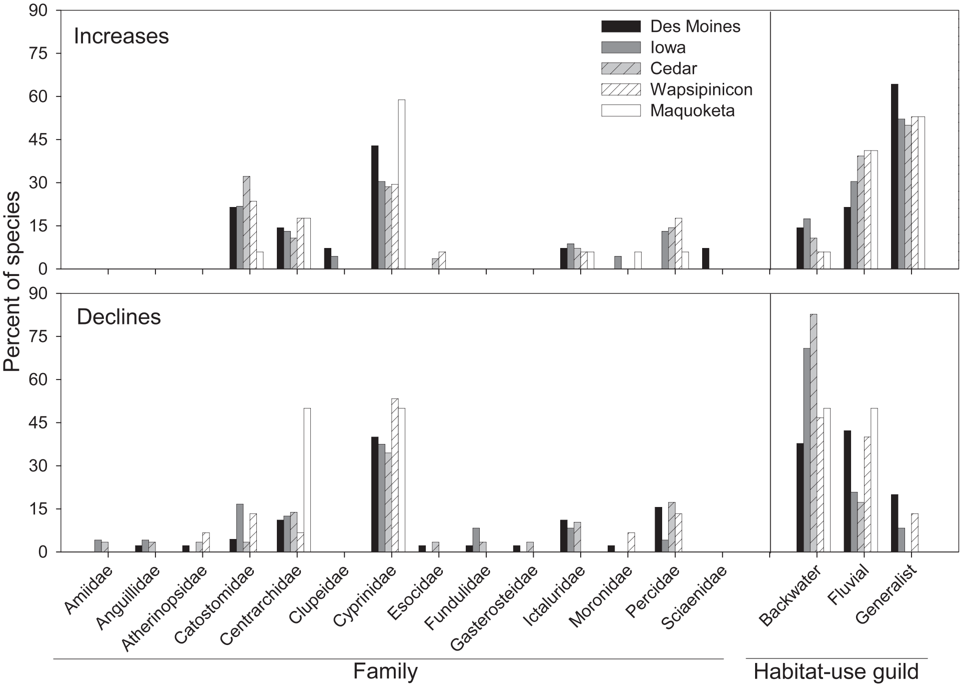

FIG. 3.—Increasing and declining trends in occurrence of fish described through percent of species represented in each family (left panels) and habitat-use guild (right panels) for nonwadeable river systems in Iowa. Families and habitat-use guilds were included if at least one species exhibited trends in more than one river or if more than one species exhibited change in only one river system

Historical trends of fish SGCN occurrence were unlike the trends observed using all fish species. Very few fish SGCN exhibited increasing trends or trends that showed 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

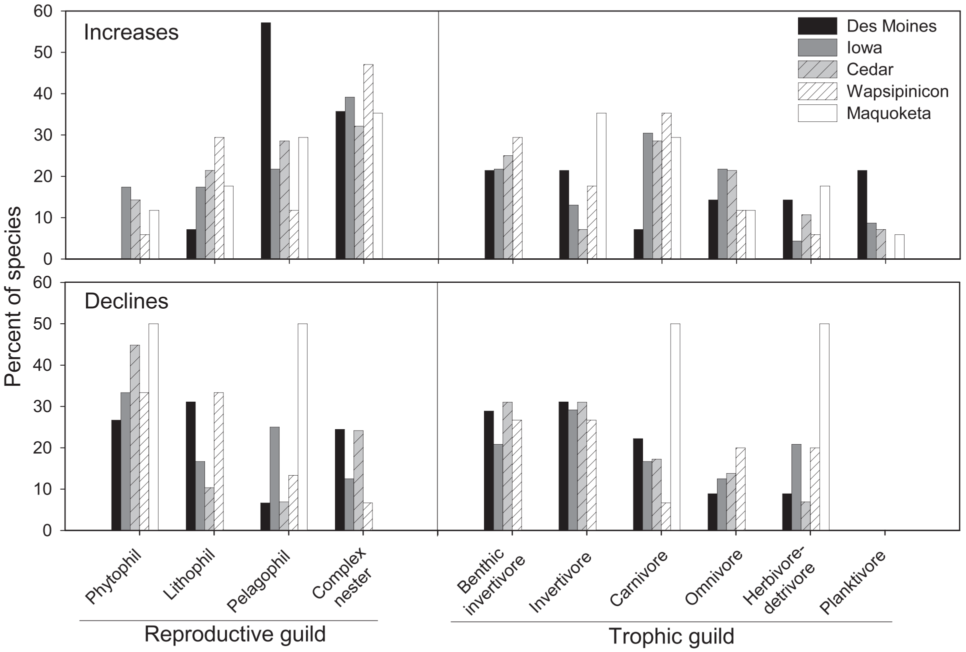

FIG. 4.—Increasing and declining trends in occurrence of fish described through percent of species represented in each reproductive (left panels) and trophic guild (right panels) for nonwadeable river systems in Iowa. Reproductive and trophic guilds were included if at least one species exhibited changes in more than one river or if more than one species exhibited change in only one river

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 phytophilic spawners. Phytophilic 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 planktivorous 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 historical (AU = 0.92) and recent cluster (AU = 0.95). The historical 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 historical 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 historical assemblage in the Maquoketa River exhibited only a low similarity with the ichthyofauna in the historical cluster while the historical 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 historical 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.

Historical 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.

Principal coordinate analysis characterized differences in multivariate dispersion among river faunas from each assessment period (Fig. 7A). Historical river faunas exhibited higher

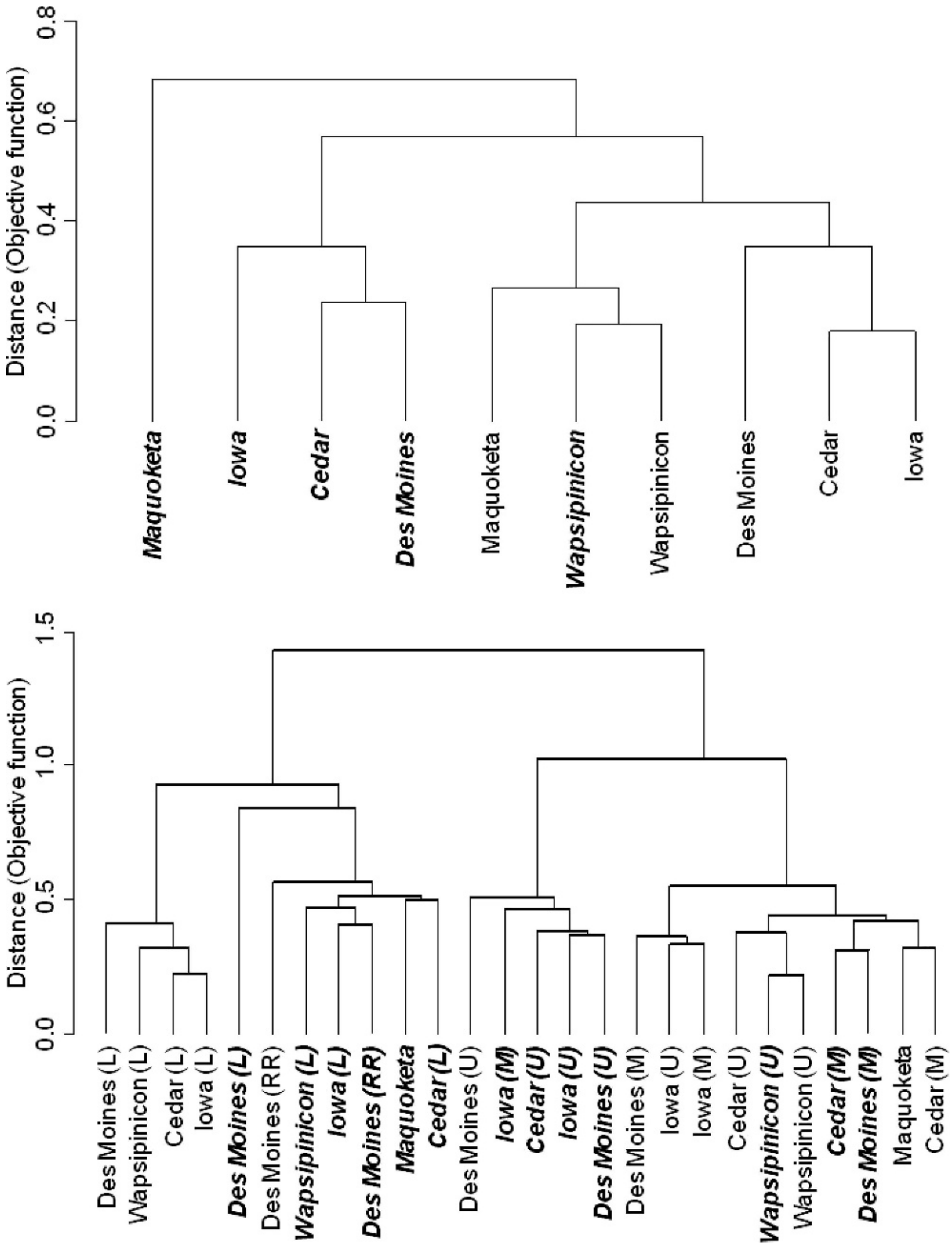

FIG. 5.—Cluster dendrograms describing similarities and differences among historical (bold-italic font) and recent (regular font) fish assemblages in rivers (top dendrogram) and 8-digit basin (HUC-8) delimited river sections (bottom dendrogram) using Jaccard's distance matrices for nonwadeable river systems in Iowa

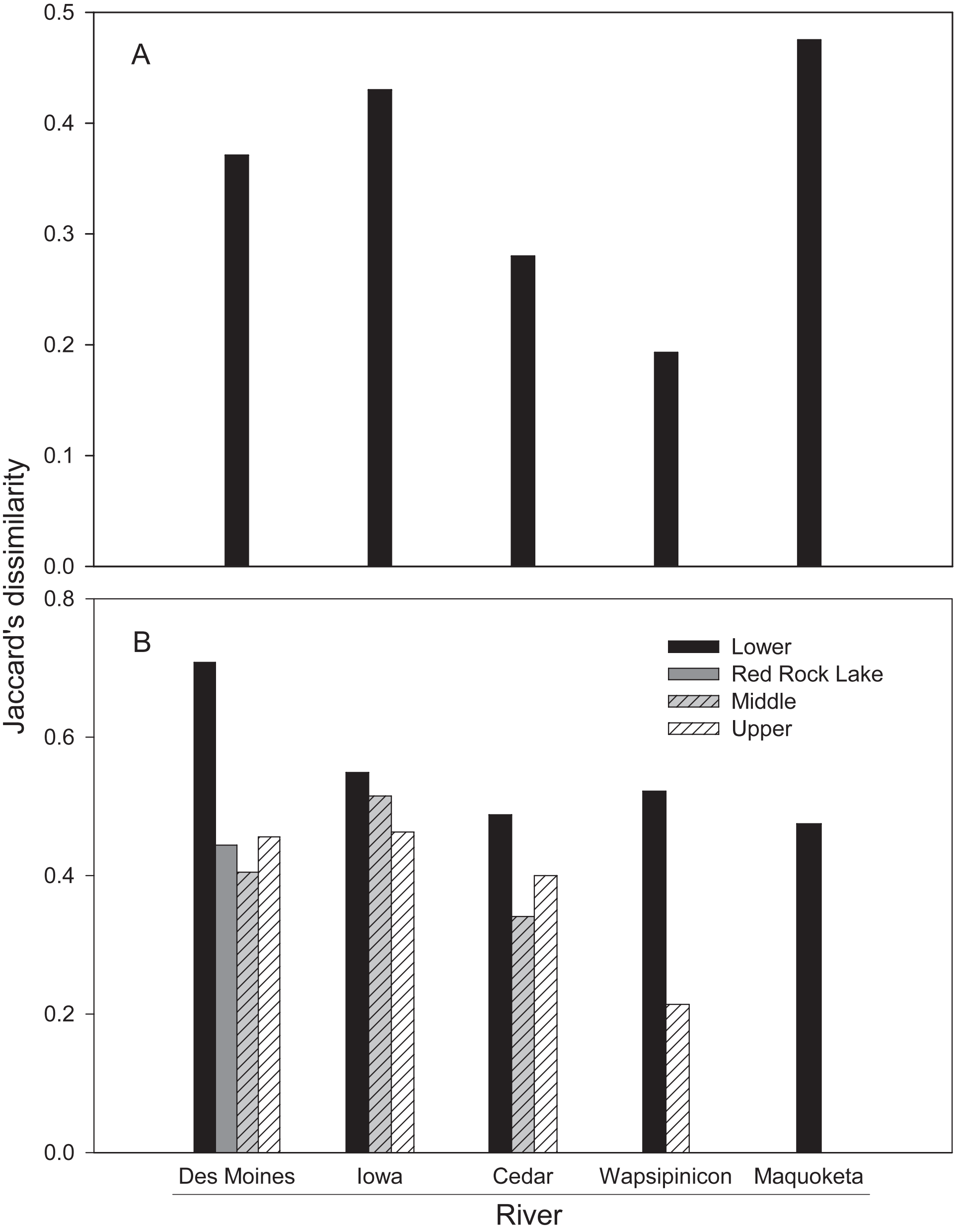

FIG. 6.—Species turnover described by Jaccard's percent dissimilarities in rivers (**A**) and 8-digit basin (HUC-8) delimited river sections (**B**) from historical (1884–1969) to recent (1990–2011) assessment periods for nonwadeable river systems in Iowa

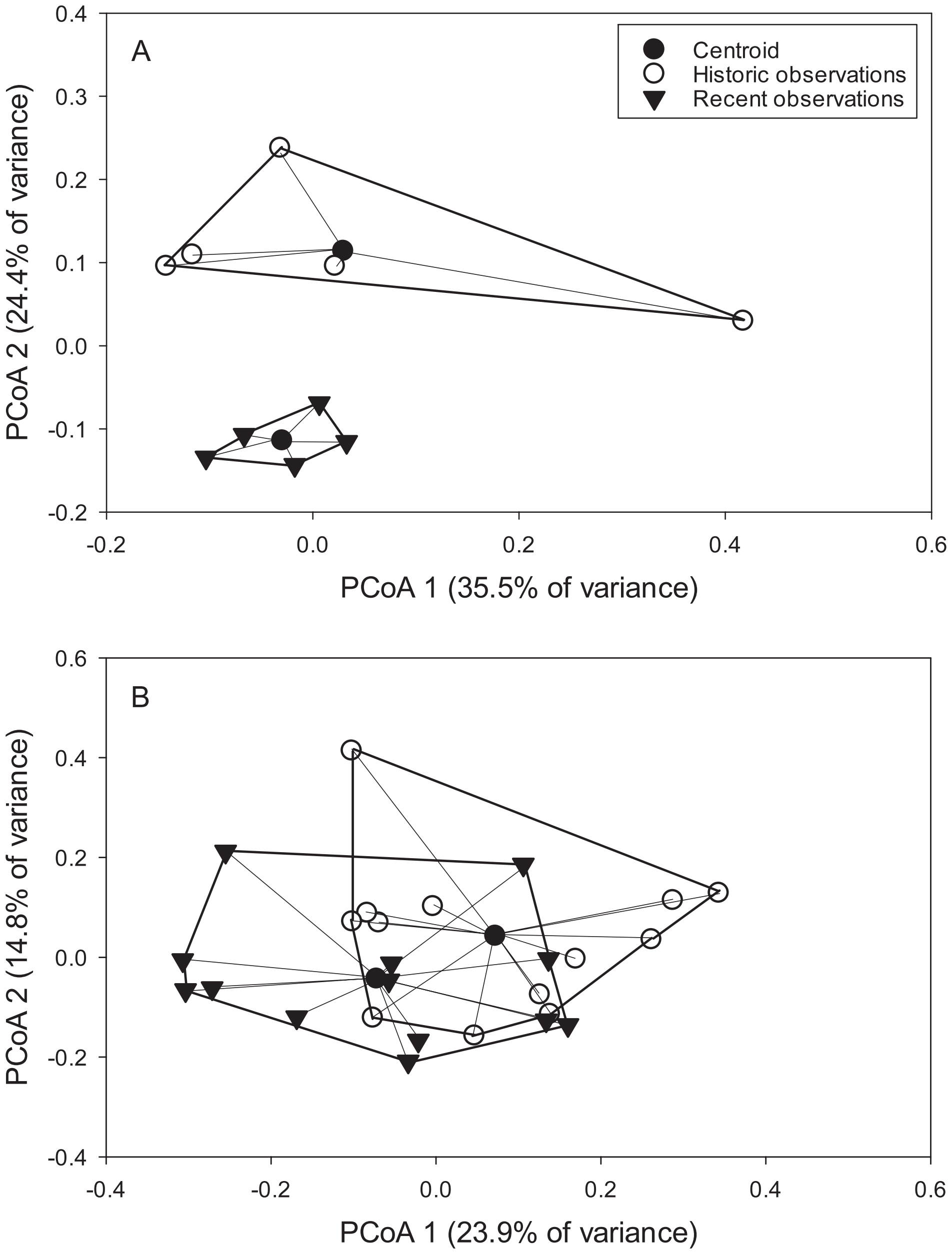

FIG. 7.—Principle coordinate analysis ordinations comparing multivariate beta dispersion among fish assemblage observations in rivers (**A**) and 8-digit basin (HUC-8) delimited river sections (**B**), between historical (1884–1969) and recent (1990–2011) assessment periods for nonwadeable river systems in Iowa

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 a slight temporal increase in faunal similarity.

Principal coordinate analysis characterized minor variation by multivariate beta dispersion among HUC-8 ichthyofauna from each assessment period (Fig. 7B). Historical 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

Historical 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 in the Wapsipinicon River and ambiguous in the Maquoketa River. The results indicate that the Maquoketa River had the largest temporal change in species composition, yet this result was confounded due to the lack of historical sampling effort and the high number of recently detected species in this river. Hence, long-term changes in fish assemblage structure in the Maquoketa River are relatively uncertain. Overall, 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 declines 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. The loss of connectivity to floodplain habitats has been directly attributed to channelization practices and to sediment aggradation, as fluvial processes become altered in response to flow disturbance (Sparks, 1995; Bunn and Arthington, 2002). In addition to the loss of connectivity, off-channel channel habitats can be completely filled with fine sediments that deposit after flood events (Menzel, 1983; 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 diaphanus*) 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.*, (2013) demonstrated similarly large differences between upstream and downstream fish assemblages in recent fish collections in Iowa. Downstream temporal turnover reflected species declines or extirpations, expansions, and recent detections (Roberts and Hitt, 2010). The local extirpations of 13 backwater species (*e.g.,* blacknose shiner and black bullhead *Ameiurus melas*) and eight fluvial specialists (*e.g.,* hornyhead chub *Nocomis biguttatus* and blackside darter *Percina maculata*) in downstream river sections potentially indicate a historical 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 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 explain 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 considerably alters the trophic structure of local fish assemblages in many Midwestern lotic systems with 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 declined in altered fluvial environments and were 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). Although our results indicate that certain groups of species have expanded, possible temporal increases in gear efficiency have occurred and influenced our results. Due to the lack of catchability estimates, it is be impossible to quantify changes in gear efficiency. Therefore, our inferences on species expansions should be interpreted with caution. In contrast we have high confidence in our inferences on species declines.

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 historical 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 historical 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 historical 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.

Acknowledgments.—We thank Anna Loan-Wilsey, Gregory Gelwicks, Greg Simmons, Tom Wilton, John Olson, Karen Kinkead, others at Iowa Department of Natural Resources for providing data, guidance, and support. We also thank Michael Colvin, Jesse Fischer, Maria Dzul, Anthony Sindt, Bryan Bakevich, Joshua McCormick, and the Quist lab at University of Idaho for their technical guidance and input. Steve Chipps, Mark Pyron, and two anonymous reviewers provided helpful comments on an earlier version of the manuscript. 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).

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SUBMITTED 21 MARCH 2013 ACCEPTED 16 SEPTEMBER 2013