Influential Environmental Gradients and Spatiotemporal Patterns of Fish Assemblages in the Unimpounded Upper Mississippi River

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ABSTRACT.—We investigated variation of fish assemblages in response to environmental factors using Long Term Resource Monitoring Program data. Data were collected from 1993 to 2000 from five physical habitats in the unimpounded upper Mississippi River. We captured 89 species composing 18 families. Of these, 26% were fluvial specialists, 25% were fluvial dependent and 49% were generalists. The numerically dominant component of the adult fish assemblage (species accounting for >10% of total catch) accounted for 50% of the assemblage and was comprised of only three species: gizzard shad (*Dorosoma cepedianum*; 25%), common carp (*Cyprinus carpio*; 15%) and channel catfish (*Ictalurus punctatus*; 10%). The dominant component of the YOY fish assemblage was comprised of only two species, which accounted for 76% of the total catch: freshwater drum (*Aplodinotus grunniens*; 39%) and gizzard shad (37%). We used a cross-validation multivariate approach to explore how adult and young-of-the-year (YOY) assemblages varied with respect to physical habitat and environmental gradients. Furthermore, we were interested how the fish assemblages changed over time. Partial canonical correspondence analyses (pCCA) demonstrated significant effects of physical habitats. Such effects differed between young-of-the-year and adult fishes. The four main environmental gradients influencing overall assemblage structure for both age groups were river elevation, water velocity, conductivity and depth of gear deployment. Morisita's index revealed similar adult assemblage structure over time. However, the YOY assemblage present in 1995 was dissimilar from assemblages present during the other years. We speculate this is a lag effect from the backwater spawning episodes (floodpulse) that occurred with the 500-y flood in 1993. Shannon-Weiner diversity and Camargo's evenness indices were low, but stable across years for the adult assemblage, but varied across years for the YOY assemblage.

INTRODUCTION

Large river systems worldwide, such as the Mississippi (United States), Murray (Australia), Rhine (Germany) and Rhône (France) rivers, have been modified for navigation and few rivers in the United States are unregulated and/or unimpounded (Peets *et al.*, 1989; Benke, 1990; Dynesius and Nilsson, 1994). The Mississippi River is the world's third largest river in terms of drainage, world's eighth largest in terms of discharge and drains approximately 41% of the contiguous United States (Baker *et al.*, 1991). Although the Mississippi River system has undergone natural changes of large magnitude over the past millennia (*e.g.*, glaciation, geomorphic), these changes did not affect the system simultaneously and were gradual (Baker *et al.*, 1991). Man-made alterations to the system over the past centuries (*e.g.*, channelization, exotic species introductions, impoundment, agricultural pollution) have

been drastic, rapid and widespread, with unknown ecological effects and little documentation (Baker *et al.*, 1991; Gehrke *et al.*, 1995; Williams *et al.*, 1996).

If the biodiversity of native assemblages is to be conserved or protected, the impact of anthropogenic disturbances must be understood. The effects of river modifications on fish assemblages, changes in biodiversity and ecological relationships are largely unknown, mainly because results derived from many fish community studies have been based on limited temporal and/or spatial scales (Pimm, 1991; Williams *et al.*, 2002). Furthermore, most conservation efforts have been focused on a single species, such as the pallid sturgeon (*Scaphirhynchus albus*; Schlosser and Angermeier, 1995). As a result, little information is known about long-term trends in assemblage structure or the potential loss of biodiversity in large river systems, especially in the United States.

The unimpounded upper Mississippi River (UMR), from the confluence with the Missouri River to the confluence with the Ohio River, is highly modified. Large-scale alteration of the UMR began with channelization in 1878 when the U.S. Congress authorized the creation of a 1.8 m navigation channel (Rasmussen, 1979). Manmade structures, such as wing dikes, closing structures and levees, were constructed to maintain channel depth (Rasmussen, 1979). This river reach was further modified when Congress approved the creation of a low water navigation channel (Rasmussen, 1979). This project redirected water flow to the main channel and away from secondary side channels and backwater physical habitats, causing restricted flow in this river reach (Rasmussen, 1979). The unimpounded reach is almost completely isolated from its floodplain by a levee system and backwater areas are often disjoint from the main channel because of wing dikes and closing structures, resulting in an altered hydrology (Rasmussen, 1979; Pitlo, 1998). Several native species have declined or become extirpated in the UMR concurrently with the river modifications, including the pallid sturgeon (*Scaphirhynchus albus*), crystal darter (*Crystallaria asprella*) and flathead chub (*Platygobio gracilis*; Pflieger, 1997). Although impounded UMR fish assemblages have been investigated (*see* Rasmussen, 1979; Ellis *et al.*, 1979; Holland and Sylvester, 1983; Sylvester and Broughton, 1983; Holland, 1986; Johnson and Jennings, 1998), few studies have focused on the assemblage inhabiting the unimpounded reach of the UMR.

Because of the lack of information regarding fish assemblages of the unimpounded UMR, our main objective was to evaluate the assemblage of this reach and assess its associations with environmental gradients, time and physical habitats using multivariate techniques. Based on the findings of Baker *et al.*(1991), Jurada (1995), Slavík and Bartoš (2001) and Barko *et al.* (2004), we hypothesized that: (1) adult and YOY fishes would have different responses to environment gradients, (2) the 500-y flood event in 1993 influenced assemblage structure and (3) fishes do not use all physical habitats equally.

METHODS

Sampling.—We collected data on fish assemblages, environmental factors and physical habitat in the unimpounded upper Mississippi River (UMR), which is located between the confluences of the Missouri (near St. Louis, MO) and Ohio Rivers (near Cairo, IL; *see* Pitlo, 2002, Fig. 1, p. 1022). Our data were collected between river kilometers (RK) 46.7 and 128.7 from 1993 to 2000. All sampling was conducted in five physical habitats using monitoring protocol developed by the Long Term Resource Monitoring Program (LTRMP; Gutreuter *et al.*, 1995) Physical habitats included main channel border, main channel border wing dike, tributary, open side channel and closed side channel (Wilcox, 1993; Gutreuter *et al.*, 1995; Barko and Herzog, 2003). Main channel border was defined as the zone between the

FIG. 1.—Partial canonical correspondence analysis (pCCA) of species and river flow characteristics in the unimpounded Upper Mississippi River. The first two axes had eigenvalues of 0.0501 and 0.0190, respectively. Only abundant species are represented in the ordination diagram. Adults of species are identifiable by species codes beginning with the letter "a" and young-of-the-year individuals are represented by species codes beginning with the letter "j." "DEPTH" = depth at gear deployment, "CURRENT" = water velocity, "GAGE" = river elevation, and "COND" = conductivity

margins of the main navigation channel and the nearest shoreline without wing dikes (*see* Barko *et al.*, 2004, Fig. 1, p. 373). Main channel border wing dike was defined as main channel border with a wing dike as the main physical structure. Open side channels had both ends connecting with the main river channel, while closed side channels had only one end connecting with the main river channel (Barko and Herzog, 2003). Tributary physical habitat was defined as the mouth of a floodplain stream and sampling was conducted 0.8–1.4 km upstream of the confluence with the Mississippi River (Gutreuter *et al.*, 1995).

Data were collected annually during three periods (15 June–30 July; 1 August–15 September; 16 September–30 October) from using eight sampling gears: daytime electrofishing, small hoop nets, large hoop nets, trawling, gill nets, seining, fyke nets and mini-fyke nets (*see* Gutreuter *et al.*, 1995 for descriptions of gear dimensions and their manner of deployment). Sample sites were determined for each physical habitat prior to the sampling season using a geographic information system (GIS; Gutreuter *et al.*, 1995). To summarize, each site was represented by a 50 m × 50 m grid, indexed by universal transverse mercator (UTM) coordinates on 1989 infrared photos (*e.g.*, base map; J.T. Rogala, UMESC, pers. comm.). The study reach was stratified by the five physical habitat classes and the known extent of each class was delineated in the GIS database (Owens and Ruhser, 1996). Annual site locations (*e.g.*, primary sites) were randomly chosen within each habitat for each period (*e.g.*, three times per year) and sampling gear. Alternate sites were randomly chosen from grids identified within 1 km^2 of the center of each primary site. Alternate sites were located within the same habitat and used the same gear type. An alternate site was only used if the primary site was inaccessible (*e.g.*, dry or submerged wing dike; 34% of our samples).

Tributary physical habitat was limited in our study area; hence, these sites were fixed in the study. Prior to sampling fishes, we measured water temperature, Secchi transparency, water velocity, depth at gear deployment and conductivity at a single point located in the center of each site, at a depth of 0.2 m from the surface (*see* Gutreuter *et al.*, 1995). These variables were chosen because they are often reported as factors that influence fish-physical habitat associations (Jones and Hoyer, 1982; Hayes *et al.*, 1996). Water temperature was measured to the nearest 0.1 °C and conductivity was measured in µS/cm using a Labcomp digital conductivity meter. A Marsh-McBirney meter (model 201 D) was used to measure water velocity to the nearest 0.01 m/s. Depth at gear deployment was measured to the nearest 0.1 m using boat-mounted sonar. River elevation data (measured at Cape Girardeau, Missouri) were obtained from the U.S. Geological Survey for each day of sampling. All fishes were identified to species, counted and measured to the nearest mm. We separated young-of-the-year (YOY) fishes from adult fishes using reported lengths for each species following criteria developed by Barko *et al.* (2004).

Data preparation.—Before analyses, we classified species as fluvial specialists, fluvial dependants or generalists to better understand assemblage structure in this floodplain river system based on published literature and regional expertise (Kinsolving and Bain, 1993; Travnicheck *et al.*, 1995; Galat *et al.*, 2004; B. M. Burr, SIUC, pers. comm.). Fluvial specialists usually inhabit streams and rivers (*e.g.*, does not imply lotic preference), fluvial dependants inhabit a variety of waters, but need flowing water at some life history stage, and generalists can inhabit lotic and/or lentic waters (Kinsolving and Bain, 1993). We separated data based on gear type (*e.g.*, coded as indicator variables) because sampling effort differed among methods and active and passive techniques probably did not sample fishes equally (Hayes *et al.*, 1996; Lepš and Šmilauer, 2003; Barko *et al.*, 2004). Samples with incomplete data were removed from the data set (12% of the observations).

Statistical analyses.—We analyzed our data using Detrended Correspondence Analysis (DCA), Canonical Correspondence Analysis (CCA), partial Correspondence Analysis (pCCA) and a stepwise pCCA. Detrended Correspondence Analysis is an indirect gradient technique that sorts species and samples along compositional gradients (Hill and Gauch, 1980). This technique was used to identify outliers in the species data set (Lepš and Šmilauer, 2003). Canonical Correspondence Analysis is a direct gradient technique that relates species composition to explanatory variables (ter Braak, 1986). In addition, CCA is a special case of multiple regression that requires no assumption of multivariate normality, allows statistical tests based on parametric inferences and a low-dimensional representation of such relationships. Partial CCA allows one to factor-out covariables (ter Braak and Prentice, 1988; Hallgren *et al.*, 1999), while the stepwise pCCA identified environmental factors that explained significant variation in assemblage structure (Hallgren *et al.*, 1999). In our study, gradient analyses were preferable to other ordination techniques (Death, 1999) because gradient analyses give a measure of beta diversity, do not weigh all samples equally, yet allow a simultaneous ordination of samples and sites. We utilized cross validation (Hallgren *et al.*, 1999) to allow us to develop, refine and test hypotheses, as described below.

Cross-validation.—Before analyses, we randomly and equally divided the samples into two separate data sets to enable us to perform an exploratory and confirmatory analysis (*e.g.*, cross-validation; Hallgren *et al.*, 1999; Lepš and Šmilauer, 2003). Exploratory analyses were used to identify patterns in the data and develop hypotheses. Confirmatory analyses were used to test hypotheses developed during the exploratory phase (Hallgren *et al.*, 1999; Lepš and Šmilauer, 2003). Because of the large sample size (n = 1643) we were not concerned with loss of power as a result of data splitting (Lepš and Šmilauer, 2003). Species abundance

data were log (y +1) transformed and rare species were down-weighted. Samples containing extreme outliers were removed independently for each data set and the criteria for omission were assessed on the same scale/transformation as the subsequent analyses. Sample outliers were identified (>1 sd from other data points along axes 1–4) using a partial DCA with gear as a covariable. We identified outliers in the environmental data set (influence $> 14 \times$) using a pCCA with gear as a covariable (Hallgren *et al.*, 1999). We used pCCA and Monte Carlo permutation tests (n = 2000) with permutation blocks defined by the categorical variables to test for significance in the confirmatory data set (Hill and Gauch, 1980; ter Braak, 1986). All analyses were performed with the computer program CANOCO v. 4.5 with default parameters, except for scaling (ter Braak and Šmilauer, 2002). We used Hill's scaling because we were interested in inter-species relationships. Multiple comparisons were corrected using the Bonferroni technique, thus maintaining a consistent overall error rate (Sokal and Rohlf, 1995; Krebs, 1999).

Auxillary assemblage analyses.—Before calculating ecological indices and similarity matrices, samples were standardized to correct for differences in effort allocation between the years (Barko *et al.*, 2004). We randomized and re-sampled to the smallest sample size (effort allocation) per gear across years 1994 to 2000. The year 1993 was excluded because a 500-y flood event precluded sampling at densities comparable to the other years in our study. Faunal similarity among the sampling years for both adult and YOY fishes was assessed using Morisita's index (I_m) and calculations on species abundance (Morisita, 1959; Krebs, 1999). This index ranges from 0 (no similarity) to 1 (complete similarity). Wolda (1981) reported that Morisita's Index of Similarity was the best overall index to use for ecological studies because this index is independent of sample size. Ross *et al.* (1985) and Matthews *et al.* (1988) considered values greater than 0.7 for I_m indicative of relatively high similarity between two fish assemblages.

Species diversity for adult and YOY assemblages was estimated using the Shannon-Weiner Diversity (H′) index (Krebs, 1999) for each of the seven sampling years. The Shannon-Weiner Diversity Index ranges from 0 (no diversity) to log(s), where s = the number of species in the assemblage (Krebs, 1999). Washington (1984) reports that biological assemblages seldom exceeded H′ = 5. Shannon-Weiner Diversity indices were calculated using log base 2. We estimated evenness separately using Camargo's Index of Evenness (E′) because this measure is unaffected by species richness (Camargo, 1993; Smith and Wilson, 1996; Krebs, 1999). This measure has a range of 0 (species are not equally abundant and vary widely in abundance) to 1 (each species is equally abundant; Smith and Wilson, 1996; Krebs, 1999).

Results

Assemblage structure.—We captured 89 species composing 18 families (Table 1). Of these, 26% were fluvial specialists, 25% were fluvial dependent and 49% were generalists (Table 1). The numerically dominant component of the adult fish assemblage (species accounting for >10% of total catch) accounted for 50% of the assemblage and was comprised of only 3 species: gizzard shad (*Dorosoma cepedianum*; 25%), common carp (*Cyprinus carpio*; 15%) and channel catfish (*Ictalurus punctatus*; 10%). The dominant component of the YOY fish assemblage was comprised of only two species, which accounted for 76% of the total catch: freshwater drum (*Aplodinotus grunniens*; 39%) and gizzard shad (37%). Conversely, YOY fishes were most abundant in main channel borders (n = 8958), followed by closed side channels (n = 5715), open side channels (n = 3311), tributaries (n = 2448) and wing dikes (n = 1787).

Exploratory analyses.—During the exploratory phase of analysis, we performed numerous

TABLE 1.—Fish species (adult/YOY) used in confirmatory analyses. All fishes were captured from 1993–2000 in the unimpounded Upper Mississippi River in wing dike (MCBW), main channel border (MCBU), open-side channel (SCBO), closed-side channel (SCBC) and tributary (TRIB) physical habitats using hoop nets, mini-fyke nets, and daytime electrofishing

Family name	Common name - species code	Scientific name	MCBW	MCBU	TRIB	SCBO	SCBC
Petromyzontidae	Chestnut lamprey[d]–CNLP	Ichthyomyzon castaneus	3/0	2/0	3/0	0/1	4/0
Acipenseridae	Shovelnose sturgeon[s]–SNSG	Scaphirhynchus platorynchus	1/0	1/0	0/0	1/0	0/1
Lepisosteidae	Spotted gar[g]–STGR	Lepisosteus oculatus	0/0	0/0	16/0	0/0	2/0
	Longnose gar[d]–LNGR	Lepisosteus osseus	2/7	2/6	2/2	3/0	4/17
	Shortnose gar[g]–SNGR	Lepisosteus platostomus	43/0	27/12	36/3	13/5	134/6
Amiidae	Bowfin[g]–BWFN	Amia calva	0/0	0/1	0/14	0/0	0/8
Hiodontidae	Mooneye[d]–MNEY	Hiodon tergisus	0/0	0/4	0/0	6/2	1/3
	Goldeye[d]–GDEY	Hiodon alosoides	0/84	0/642	0/4	0/105	0/169
Anguillidae	American eel[d]–AMEL	Anguilla rostrata	5/0	4/0	1/0	1/0	1/0
Clupeidae	Skipjack herring[d]–SJHR	Alosa chrysochloris	6/1	27/15	3/3	7/9	3/6
	Gizzard shad[g]–GZSD	Dorosoma cepedianum	887/512	1094/2391	941/1696	595/942	1368/2577
	Threadfin shad[g]–TFSD	Dorosoma petenense	15/4	18/27	23/19	10/6	10/6
Cyprinidae	Central stoneroller[s]–CLSR	Campostoma anomalum	1/1	7/1	0/0	0/2	0/0
	Goldfish[g]–GDFH	Carassius auratus	0/0	0/0	0/1	0/0	0/0
	Grass carp[d]–GSCP	Ctenopharyngodon idella	1/0	0/0	3/0	0/0	2/0
	Red shiner[g]–RDSN	Cyprinella lutrensis	194/5	121/0	10/0	28/2	1011/95
	Spotfin shiner[s]–SFSN	Cyprinella spiloptera	4/0	0/0	0/0	0/0	2/0
	Blacktail shiner[g]–BTSN	Cyprinella venusta	15/0	3/0	14/2	0/0	16/0
	Common carp[g]–CARP	Cyprinus carpio	297/4	492/52	1141/3	152/246	888/15
	Mississippi silvery minnow[d]–SVMW	Hybognathus nuchalis	0/7	4/2	0/0	1/1	10/5
	Plains minnow[d]–PNMW	Hybognathus placitus	0/0	0/1	0/0	0/0	1/1
	Silver carp[d]–SVCP	Hypophthalmichthys molitrix	0/0	0/8	0/0	0/1	0/2
	Bighead carp[d]–BHCP	Hypophthalmichthys nobilis	0/7	3/2	2/6	0/0	0/7
	Bleeding shiner[s]–BDSN	Luxilus zonatus	0/0	1/0	0/0	0/0	0/0
	Speckled chub[s]–SKCB	Macrhybopsis aestivalis	1/0	11/5	0/0	0/0	7/10
	Sicklefin chub[s]–SFCB	Macrhybopsis meeki	0/0	1/0	0/0	0/0	0/0
	Silver chub[s]–SVCB	Macrhybopsis storeriana	1/6	7/18	0/1	2/0	14/7
	Golden shiner[g]–GDSN	Notemigonus crysoleucas	0/0	0/1	0/0	0/0	0/0
	Emerald shiner[g]–ERSN	Notropis atherinoides	251/187	443/100	45/12	238/6	591/147
	River shiner[s]–RVSN	Notropis blennius	6/6	95/10	1/0	2/3	11/14

TABLE 1.—Continued

Family name	Common name - species code	Scientific name	MCBW	MCBU	TRIB	SCBO	SCBC
	Bigeye shiner[s]–BESN	*Notropis boops*	2/0	0/0	0/0	0/0	0/0
	Sand shiner[s]–SNSN	*Notropis stramineus*	0/0	0/0	0/0	0/1	0/2
	Silverband shiner[s]–SBSN	*Notropis shumardi*	34/8	41/90	21/14	12/9	49/131
	Mimic shiner[s]–MMSN	*Notropis volucellus*	1/0	0/0	0/0	0/0	0/0
	Channel shiner[s]–CNSN	*Notropis wickliffi*	28/129	56/451	2/53	9/0	46/566
	Pugnose minnow[g]–PGMW	*Opsopoeodus emiliae*	0/2	0/1	0/0	0/0	0/0
	Bluntnose minnow[g]–BNMW	*Pimephales notatus*	1/4	1/6	1/4	0/0	1/10
	Bullhead minnow[g]–BHMW	*Pimephales vigilax*	8/8	20/3	16/1	2/0	19/7
	Creek chub[g]–CKCB	*Semotilus atromaculatus*	0/0	0/0	0/0	0/1	0/0
Catostomidae	River carpsucker[g]–RVCS	*Carpiodes carpio*	15/9	86/35	226/4	85/13	115/23
	Quillback[s]–QLBK	*Carpiodes cyprinus*	1/0	0/1	0/3	1/0	0/3
	Blue sucker[s]–BUSK	*Cycleptus elongatus*	7/0	2/5	0/0	9/3	1/1
	Smallmouth buffalo[g]–SMBF	*Ictiobus bubalus*	40/1	292/0	191/1	62/1	283/1
	Bigmouth buffalo[g]–BMBF	*Ictiobus cyprinellus*	2/3	7/34	35/8	2/65	49/3
	Black buffalo[g]–BKBF	*Ictiobus niger*	10/0	31/0	145/1	4/12	89/0
	Golden redhorse[d]–GDRH	*Moxostoma erythrurum*	1/0	0/0	0/0	0/0	0/0
	Shorthead redhorse[d]–SHRH	*Moxostoma macrolepidotum*	0/0	1/0	0/0	5/0	0/0
	River redhorse[d]–RVRH	*Moxostoma carinatum*	0/0	0/0	0/0	1/0	0/0
Ictaluridae	Black bullhead[g]–BKBH	*Ameiurus melas*	0/0	1/0	1/0	1/0	0/0
	Yellow bullhead[g]–YLBH	*Ameiurus natalis*	0/0	0/0	0/0	0/0	0/1
	Blue catfish[s]–BLCF	*Ictalurus furcatus*	10/0	42/0	0/0	1/1	18/0
	Channel catfish[g]–CNCF	*Ictalurus punctatus*	268/141	578/88	90/4	344/57	553/104
	Stonecat[s]–STCT	*Noturus flavus*	0/2	1/0	0/0	1/1	0/0
	Tadpole madtom[g]–TPMT	*Noturus gyrinus*	0/0	0/0	0/1	0/0	0/0
	Freckled madtom[s]–FKMT	*Noturus nocturnus*	9/5	2/3	0/1	5/3	0/0
	Flathead catfish[d]–FHCF	*Pylodictis olivaris*	108/0	87/0	35/0	45/0	83/0
Esocidae	Muskellunge[g]–MSKG	*Esox masquinongy*	0/0	0/0	0/1	0/0	0/0
Percopsidae	Trout perch[g]–TTPH	*Percopsis omiscomaycus*	0/0	0/1	0/0	0/0	0/0
	Pirate perch[d]–PRPH	*Aphredoderus sayanus*	0/0	0/1	0/0	0/1	1/0
Fundulidae	Blackstripe topminnow[g]–BTTM	*Fundulus notatus*	0/1	0/0	35/3	0/0	11/0
	Blackspotted topminnow[g]–BPTM	*Fundulus olivaceus*	2/0	0/0	2/0	0/0	0/0
Poeciliidae	Western mosquitofish[g]–MQTF	*Gambusia affinis*	8/3	11/6	25/6	3/0	49/22
Atherinidae	Brook silverside[g]–BKSS	*Labidesthes sicculus*	1/2	10/4	12/109	0/1	29/21

TABLE 1.—Continued

Family name	Common name - species code	Scientific name	MCBW	MCBU	TRIB	SCBO	SCBC
	Inland silverside^g–INSS	Menidia beryllina	0/0	7/0	2/0	2/0	0/0
Percichthyidae	White bass^d–WTBS	Morone chrysops	42/100	37/199	22/234	21/35	56/152
	Yellow bass^d–YWBS	Morone mississippiensis	0/1	1/0	1/1	1/0	0/0
	Striped bass^d–SDBS	Morone saxatilis	0/0	0/1	0/0	0/0	0/0
Centrarchidae	Flier^g–FLER	Centrarchus macropterus	0/0	1/0	0/0	0/0	0/0
	Warmouth^g–WRMH	Lepomis gulosus	1/6	1/8	12/4	0/0	2/1
	Orangespotted sunfish^g–OSSF	Lepomis humilis	25/1	15/0	135/4	3/0	52/2
	Bluegill^g–BLGL	Lepomis macrochirus	191/0	163/84	538/20	18/0	424/423
	Longear sunfish^g–LESF	Lepomis megalotis	1/1	0/0	2/4	0/1	5/2
	Green sunfish^g–GNSF	Lepomis cyanellus	10/0	61/0	10/0	5/1	33/2
	Spotted bass^g–STBS	Micropterus punctulatus	14/0	6/0	107/6	0/1	21/3
	Largemouth bass^g–LMBS	Micropterus salmoides	9/0	2/0	73/0	1/1	5/0
	White crappie^g–WTCP	Pomoxis annularis	76/93	17/30	125/25	0/5	17/23
	Black crappie^g–BKCP	Pomoxis nigromaculatus	38/16	6/4	57/2	2/0	19/3
Percidae	Mud darter^d–MDDR	Etheostoma asprigene	0/0	1/0	38/1	1/1	0/2
	Bluntnose darter^d–BNDR	Etheostoma chlorosoma	1/0	1/0	36/0	0/0	2/0
	Slough darter^s–SLDR	Etheostoma gracile	0/0	0/0	0/2	0/0	0/0
	Johnny darter^d–JYDR	Etheostoma nigrum	0/0	0/1	0/1	0/0	0/0
	Orangethroat darter^s–OTDR	Etheostoma spectabile	1/0	0/0	0/0	1/0	0/0
	Banded darter^s–BDDR	Etheostoma zonale	0/0	0/0	0/3	0/0	0/0
	Logperch^g–LGPH	Percina caprodes	0/0	0/2	0/4	0/2	0/5
	Slenderhead darter^s–SHDR	Percina phoxocephala	0/0	0/0	0/0	0/0	0/3
	Dusky darter^s–DYDR	Percina sciera	0/0	0/0	0/3	0/0	0/0
	River darter^s–RRDR	Percina shumardi	0/2	1/3	0/0	0/1	0/1
	Sauger^g–SGER	Stizostedion canadense	2/3	7/21	4/4	3/6	8/8
Sciaenidae	Freshwater drum^g–FWDM	Aplodinotus grunniens	113/416	192/4577	34/146	101/1728	238/1090
			2813/1787	4151/8958	4273/2448	1800/3311	6389/5715

^s denotes fluvial specialist
^d denotes fluvial dependant
^g denotes fluvial generalist

analyses and a summary of our findings follows. We did not include samples collected using seining, gill netting fyke netting or trawling in analyses because these gears were not sampled across all physical habitats or with annual consistency (n = 164; 19% samples removed from confirmatory data set). Initial DCA and CCA analyses revealed interpretable results when data were log-transformed, species were downweighted and Hill's scaling was used. Hence, we used these transformations for all subsequent analyses. Initial DCA and CCA analyses contained outliers (<1 % of samples) and enabled us to establish criteria for removal to produce meaningful results. In addition, we found the first two axes were the most interpretable, thus the only axes examined in confirmatory analyses. We performed a CCA analysis with all variables, but results were not easily interpreted. The analysis did indicate that gear types, sampling period, physical habitat and year were influential (*i.e.*, long axes) and, thus, were factored out of subsequent analyses as covariables. We also noticed a separation between YOY and adults of species in ordination space, suggesting adults and YOY of some species may be using different physical habitats and environmental cues. We used a stepwise CCA to identify environmental variables that explained variation in assemblage structure. These exploratory analyses enabled us to develop six hypotheses, some with subsets, to test during the confirmatory phase of analysis (Table 2).

Confirmatory analyses.—Our confirmatory data set was composed of 4600 individuals from wing dikes, 13,110 individuals from main channel borders, 5112 individuals from open side channels, 12,075 individuals from closed side channels and 6721 individuals from tributaries comprising 823 sampling episodes (Table 1). Of these, 235 samples were taken at wingdikes, 118 in main channel borders, 95 in open side channels, 272 in closed side channels and 103 in tributaries. For visual clarity, we only display abundant taxa on subsequent biplots (*e.g.*, species weights ≥1). In addition, a number of species, though present, had low abundances (Table 1). Some species are obviously rare, such as plains minnow (*Hybognathus placitus*), mooneye (*Hiodon tergisus*) and Mississippi silvery minnow (*H. nuchalis*), while others had a low probability of collection because of the gears deployed, such as shovelnose sturgeon (*Scaphirhynchus platorynchus*) and sicklefin chub (*Macrhybopsis meeki*). Therefore, we made no attempt to draw conclusions about the status of such species in the system.

Relating environmetal gradients to species.—All confirmatory tests were significant even after the Bonferroni correction. The four significant environmental variables (identified in the exploratory phase of analysis: river elevation, conductivity, depth at gear deployment and water velocity) collectively explained 10% of the total variation in the combined adult and YOY fish assemblage (Fig. 1). Axis 1 represented a water velocity/conductivity gradient (eigenvalue = 0.0501). The majority of species fell within the intermediate to low velocity/ conductivity range. Adult and YOY Centrarchidae were associated with slower water velocities, while fluvial specialist/dependant species, such as adult flathead catfish (*Pylodictis olivaris*), YOY goldeye (*Hiodon alosoides*), YOY silver carp (*Hypophthalmichthys molitrix*) and adult blue catfish (*Ictalurus furcatus*) were associated with faster water velocities. Axis 2 (eigenvalue = 0.019) separated the species based on river stage, depth of gear deployment and water velocity. Young-of-the-year silver carp, adult blue catfish and YOY brook silverside (*Labidesthes sicculus*) tended to associate with higher river stage, deeper gear sets and lower conductivity, while adult green sunfish (*Lepomis cyanellus*), YOY sauger (*Stizostedion canadense*) and adult river carpsucker (*Carpiodes carpio*) tended to associate with lower river stages, shallower gear sets and higher conductivity. Higher conductivity occurred in the summer months when river gage and depth of gear deployment were lower and was mostly an influence from tributaries (*e.g.*, Big Muddy River). The separation of species on this axis is likely because of seasonal differences in use of floodplain or backwater areas for spawning and/or nurseries.

Table 2.—Null hypotheses developed during the exploratory phase and statistical results from the confirmatory phase of data analysis. Bonferroni adjustments were used to adjust for multiple comparisons (n = 13) and significance testing was done using Monte Carlo permutations (N = 2000)

Hypothesis	Type of analysis	Data used	P-value	Corrected P- value
1. Fish assemblages did not differ between the sampling periods given year, habitat, and gear.				
	pCCA	YOY and adults	<0.0005	<0.007
2a. Fish assemblages did not differ between the sampling years given period, habitat, and gear.				
	pCCA	YOY and adults	<0.0005	<0.007
2b. Adult fish assemblages did not differ between the sampling years given period, habitat, and gear.				
	pCCA	adults	<0.0005	<0.007
2c. Young-of-the-year fish assemblages did not differ between the sampling years given period, habitat, and gear.				
	pCCA	YOY	<0.0005	<0.007
3a. Fish assemblages did not differ in the physical habitats given gear, year, and period.				
	pCCA	YOY and adults	<0.0005	<0.007
3b. Adult fish assemblages did not differ in the physical habitats given gear, year, and period.				
	pCCA	adults	<0.0005	<0.007
3c. Young-of-the-year fish assemblages did not differ in the physical habitats given gear, year, and period.				
	pCCA	YOY	<0.0005	<0.007
4. The river-flow variables did not explain a significant amount of residual variation in species composition given year, gear, and period. These four variables were identified during the exploratory phase of analysis using a stepwise CCA.				
	pCCA	YOY and adults	<0.0005	<0.007
5. Fish assemblages did not vary at different structures or substrates (i.e., wing dike, closing, riprap, snag, silt, clay/silt) given year, gear, and period.				
	pCCA	YOY and adults	<0.0005	<0.007
6. Sampling gears did not capture different fish assemblages given period, year, and habitat.				
	pCCA	YOY and adults	<0.0005	<0.007

Relating habitats to species (adults).—Adults of many species were associated with wing dike, closed side channel and tributary physical habitat, which tend to have lower velocities (Fig. 2a) when compared to main channel borders and open side channels. Physical habitat explained 18% of the total variation in the adult fish assemblage. Axis 1 (eigenvalue = 0.1200) separated closed side channel, open side channel, wing dike and main channel border aquatic areas from tributaries. Axis 2 (eigen value = 0.0290) separated closed side channels from the remaining physical habitats. Tributary and closed side channel aquatic areas may be unique physical habitats to adult fishes compared to the other three physical habitats investigated. Centrarchidae were associated with tributary areas, generalists, such as bigmouth buffalo (*Ictiobus cyprinellus*) and red shiner (*Cyprinella lutrensis*) were associated with closed side channels, while fluvial specialist/dependants such as skipjack herring (*Alosa chrysochloris*), river shiner (*Notropis blennius*) and flathead catfish were most abundant in wing dike areas. Most other species had no strong habitat associations.

Relating habitats to species (YOY).—Although patterns were not strong for many YOY fishes, several species associated with main channel border and closed side channel physical habitats (Fig 2a). Physical habitats explained 12% of the variation in the YOY fish assemblage. Axis 1 (eigenvalue = 0.0673) separated tributaries from the remaining physical habitats and axis 2 (eigenvalue = 0.0264) separated closed side channels from the remaining
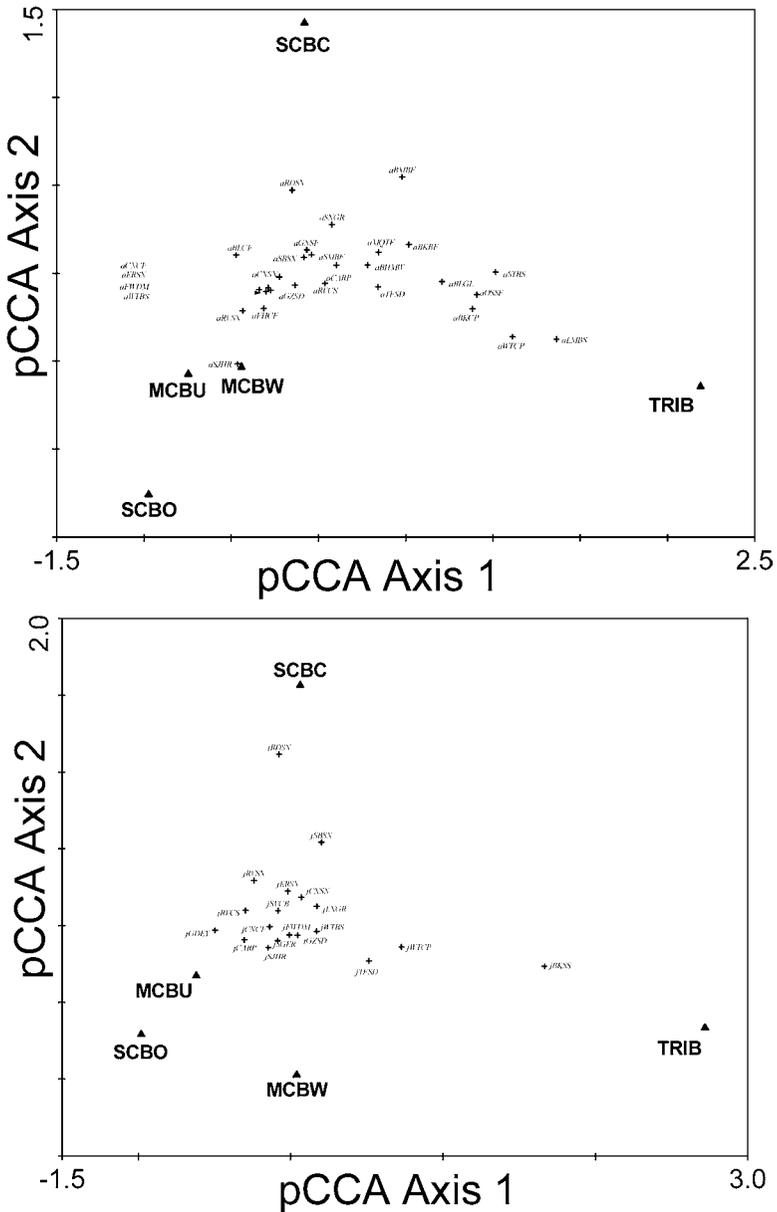
FIG. 2.—Partial canonical correspondence analyses (pCCA) of physical habitats and species for the unimpounded Upper Mississippi River. "MCBU" =main channel border, "MCBW" =wing dike, "SCBC" = closed side channel, "SCBO" = open side channel, and "TRIB" = tributary. (A) Species scores for abundant adult species. The first two axes had eigenvalues of 0.1200 and 0.0290, respectively. (B) Species scores for abundant young-of-the year fishes. The first two axes had eigenvalues of 0.0673 and 0.0264, respectively

TABLE 3.—Morisita's Indices of Similarity for fishes (adult/YOY) captured in the unimpounded Upper Mississippi River from 1994–2000

Year	1994	1995	1996	1997	1998	1999	2000
1994	1.00/1.00	0.81/0.53	0.87/0.78	0.83/0.74	0.98/0.79	0.96/0.81	0.98/0.76
1995		1.00/1.00	0.87/0.50	0.71/0.17	0.81/0.69	0.76/0.47	0.79/0.47
1996			1.00/1.00	0.92/0.80	0.87/0.94	0.89/0.97	0.82/0.96
1997				1.00/1.00	0.84/0.71	0.87/0.85	0.77/0.83
1998					1.00/1.00	0.97/0.95	0.97/0.96
1999						1.00/1.00	0.93/0.98
2000							1.00/1.00

physical habitats, suggesting tributaries and closed side channels may also be unique physical habitats for YOY fishes. Fluvial specialist/dependant and generalist YOY of fish species were associated with main channel borders (*e.g.*, goldeye, skipjack herring, common carp) and closed side channels (*e.g.*, red shiner, silverband shiner; *Notropis shumardi*). The generalist, brook silverside, had the strongest association with tributaries.

Auxiliary assemblage metrics.—Morisita's index revealed a relatively similar adult fish assemblage over the seven years analyzed (Table 3), because values calculated for each year of sampling were all greater than 0.7 (Ross *et al.*, 1985; Matthews, 1988). However, the YOY assemblage present in 1995 was relatively dissimilar from all other study years. The YOY assemblage has been relatively similar since 1996 and it appears that this may have been the representative assemblage prior to the flood disturbance because the assemblage in 1994 is relatively similar to the assemblages present from 1996–2000.

For adults, the Shannon-Weiner Diversity Index and Camargo's Evenness Metric remained relatively stable, but low, over the 7-y analyzed (Table 4). Ranges were 3.3–3.9 and 0.18–0.26, respectively. However, YOY fishes did not follow a similar pattern. Heterogeneity and evenness were variable and values were lowest in 1995 and 1998 (ranges were 1.4–3.0 and 0.08–0.19, respectively).

DISCUSSION

The unimpounded UMR differs from the modified rivers in Europe that have been more extensively studied (*see* Copp, 1989; Scheimer and Spindler, 1989; Jurajda, 1995), mainly because of the reduction in connectivity of backwater and floodplain habitats with the main river channel which reduces available habitat for spawning, nursery and overwintering sites (Jurajda, 1995). The associations we found between fishes and lower velocity physical habitats supports the common contention that fluvial species need backwater areas for life history requirements (*i.e.*, side channel and tributary). Barko *et al.* (2004) and Barko and Herzog (2003) suggested that fishes in the unimpounded UMR use wing dike scour holes and side channels as surrogate low velocity habitat because other types of backwater habitat (*e.g.*, flooded terrestrial) is scarce in this reach. However, further investigation is needed, especially regarding over-wintering and flooded terrestrial use by fishes. Such information could also fill much needed information gaps regarding life histories of many fluvial specialist and dependant species (Galat and Zweimueller, 2001). Floyd *et al.* (1984) and Mills and Mann (1985) reported that many YOY fishes use main channel border areas for nurseries in large river systems. Our study identified associations between some YOY fishes and main channel borders; however, the magnitude of association was low for many species. Baker *et al.* (1991) reported low associations between fish assemblages and physical habitats in the lower Mississippi River. We also found low associations between fish assemblages

TABLE 4.—Shannon-Weiner Diversity Indices (H') and Carmargo's Evenness Metrics (E') for adult and YOY fishes captured in the unimpounded UMR from 1994–2000

Year	H' for Adults	E' for adults	H' for YOY	E' for YOY
1994	3.61	0.20	3.03	0.15
1995	3.83	0.26	1.41	0.08
1996	3.95	0.24	2.16	0.12
1997	3.80	0.25	2.93	0.16
1998	3.32	0.20	1.89	0.09
1999	3.63	0.21	3.03	0.19
2000	3.33	0.18	2.00	0.10

(adult and YOY) and physical habitats of the unimpounded UMR, likely because this river reach is dominated by a few generalist species. The low relative abundance of fluvial species (*e.g.*, dependents and specialists) compared to generalists suggests that the unimpounded UMR is degraded and could be moving toward a system dominated by tolerant species (*e.g.*, generalists; Kinsolving and Bain, 1993). The magnitude of degradation in our study reach is unknown as well as the source(s). Plausible causes are altered flow regimes from navigation channel maintenance structures (*e.g.*, wing dikes and closing structures; Kinsolving and Bain, 1993), upstream impoundments (Peets, 1984), hydrologic variability (Williams *et al.*, 2002), low recruitment by fishes because of habitat loss/degradation and/or reduction in flood-pulse and non-floodpulse connectivity.

The unimpounded UMR is the most hydrologically dynamic reach of the UMR and fluctuations in river elevation change rapidly and often (Gutreuter *et al.*, 1997). It appears that the flood of 1993 was a major environmental disturbance that influenced the assemblage structure of the UMR, especially YOY fishes. We postulate that fishes requiring backwater areas for spawning and nursery habitats, such as those in Centrarchidae (Pflieger, 1997), had high recruitment this year because the large-scale flood event provided accessibility to flooded terrestrial areas. The 1993 cohort would be sexually mature for many species in 1995 and their increased reproductive effort could explain the dissimilarity among the YOY assemblages when compared to the assemblage present in 1995. Fluctuating diversity and evenness indices for YOY assemblages likely reflect cyclic patterns in recruitment because of inter-annual variability within the system.

Although this river reach does not directly experience altered flow regimes by lock and dams, flow regimes have been altered by wing dikes, levees and closing structures (Rasmussen, 1979). These structures direct flow from offshore areas into the main channel to maintain the low water navigation channel (Rasmussen, 1979). Channelization and other anthropogenic disturbances may increase the hydrologic variability of the river and lead to altered assemblage structure over time (Williams *et al.*, 2002), as predicted by the intermediate disturbance hypothesis (Connell, 1978). This theory predicts greatest species richness at intermediate levels of disturbance. Death and Winterborne (1995) reported greatest invertebrate evenness at sites with intermediate disturbance. In our study, species evenness was low for both adult and YOY fishes across all study years, which may be indicative of high levels of disturbance in this river reach. Disturbances, such as channelization, have lead to altered hydrographs and sediment transport (Hesse and Mestl, 1993), reduced floodplain connectivity (Vannote *et al.*, 1980), altered main channel width, depth and direction (Conner *et al.*, 1983), restricted natural river meandering (Rasmussen, 1979; Yin and Nelson, 1995; Pitlo 1998) and degraded main channel physical habitats (Mueller, 1977).

We found that river elevation and water velocity were two of the main gradients significantly influencing both adult and YOY fish assemblages. We speculate this is because floodpulse and non-floodpulse connectivity has declined in the unimpounded UMR. Non-floodpulse related connectivity provides low velocity habitats throughout much of the year. This type of connectivity has been reduced by channel training structures and to some extent, altered hydrology. Fluvial specialists (*e.g.*, blue catfish and freckled madtom; *Noturus nocturnus*) and fluvial dependants (*e.g.*, skipjack herring and flathead catfish) tend to be represented by fewer individuals than generalist (*e.g.*, common carp, channel catfish and emerald shiner; *N. atherinoides*). We speculate that loss of low velocity off-channel areas effectively increases annual mortality rates of species requiring such areas during some or all stages of their life history. Conversely, the significance of river elevation and water velocity gradients to fish assemblage structure may be because of the lack of floodpulse connectivity between the river channel and the floodplain, which adversely affects the reproduction and recruitment of species such as bowfin, paddlefish and freshwater drum (Beckett and Pennington, 1986; Baker *et al.*, 1991). This type of connectivity has been reduced because of the extensive levee system in this river reach and to some extent, altered hydrology. The extent to which the reduction of these two types of connectivity are influencing assemblage structure are largely uncertain, yet offer two alternate, though somewhat related hypotheses that should be investigated further.

Our study revealed patterns that are fundamental to the understanding of the ecology of fishes in large modified rivers. The knowledge of habitat use by fishes and influential environmental gradients are necessary for biological conservation and habitat restoration. Although river modifications occur in the unimpounded UMR on a continuous basis, few studies have investigated pre-and-post modification assemblage patterns or the spatial and/or temporal effects on biological organisms. In lieu of such studies, our findings can help managers and scientists make more informed decisions regarding focused research, dredging, wing dike creation/modification, habitat restoration and side-channel maintenance.

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