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Hydrological variation and fish assemblage structure in the middle Wabash River

Mark Pyron* & Thomas E. Lauer
Aquatic Biology and Fisheries Center, Department of Biology, Ball State University, Muncie, IN 47306, U.S.A.
*(*Author for correspondence: Tel.: + 1-765-265-8852, Fax: + 1-765-265-8804, E-mail: mpyron@bsu.edu)*

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Abstract

Two years of fish assemblage data from 28 sites in the Wabash River Indiana, were examined for relationships with environmental variables using a multivariate approach, correspondence analysis. Upstream sites had lower mean daily discharge and lower coefficient of variation of daily discharge when compared to downstream sites. Although the fish assemblage changed along this 230-km river distance gradient, patterns were in contrast to the patterns in streams with unaltered flow regimes. We compared functional variables of fish species (species traits that describe habitat, trophic, morphological, and tolerance characteristics) by examining the proportion of their occurrences along the hydrological variability gradient (upstream–downstream). The general pattern showed assemblages from hydrologically stable (upstream) sites had higher proportions of generalist species that tend to occur in small to medium streams, prefer fast current velocities, generally occur over rocky, gravel, and sand substrates, and have low silt tolerance. In addition, there was a pattern relating the hydrological/longitudinal regime and the overall morphology of species: species with higher caudal peduncle/caudal fin ratios and more fusiform body shapes occurred in higher proportion in upstream sites.

Introduction

Fish assemblages in large rivers have not been studied to the extent of those in small to medium streams. Lyons et al. (2001) provided a short list of larger river studies that characterized fish assemblages using the index of biotic integrity (IBI), and suggested that this task has been difficult due to collection limitations. This deficiency in our understanding of large rivers is problematic, as these systems typically have been overexploited for long periods of time (Sparks, 1995). Exploitation includes navigational uses, dam construction, recreational fisheries, commercial fisheries, and as a conduit for agricultural and municipal runoff and waste. Furthermore, because the largest rivers have been disproportionately degraded compared to other aquatic ecosystems (Karr et al., 1985), the complete effects of long-term exploitation of many rivers are only marginally understood.

In addition to fish assemblages of large rivers not being well understood, the study of relationships linking hydrological regimes and fish assemblages is in its infancy (Poff & Allan, 1995). The hydrological regime of large rivers has been well characterized – it is a consequence of drainage from both the terrestrial component of the watershed, and channel morphology (Leopold, 1997). Changes in morphology of the stream channel alter scouring location and produce riffle-pool sequences that differ from upstream to downstream (Poff et al., 1997). Upstream reaches have comparatively smaller pools than downstream reaches. In addition, the larger downstream pools may provide better refugia from harsh physical conditions and predators (Schlosser, 1990). Fish assemblages have been shown to change predictably with these river longitudinal changes in habitat and other associated variables (Gorman & Karr, 1978; Horwitz, 1978; Peterson & Rabeni, 2001). Poff & Allen (1995) used hydrological regimes as a template for explaining variation among fish assemblages in lotic ecosystems. This study identified hydrological variability as the most important gradient among 34 upper Midwest sites. Fish assemblages differed between hydrologically variable and hydrologically stable sites, based on a set of functionally derived characters (species traits that describe habitat, trophic, morphological, and tolerance characteristics; Poff & Allan, 1995).

The Wabash River in Indiana has been continually degraded since settlement times, principally from agricultural development and human population impacts. These historical trends appeared to reverse in 1984, when a sudden and substantial improvement in the middle Wabash River fishery was identified, continuing to the present time (Gammon, 1994, 1998). Gammon (1994) suggested these changes were due to gradual, but cumulative point source reductions in BOD loadings to the river. These findings were only made possible by his continued and ongoing fish community assessments of the river. In a comprehensive review, Gammon (1998) suggested that long-term studies on the Wabash River permitted him to: (1) relate changes in the fish communities to natural events and man-induced factors, (2) identify problem sections of the river, (3) evaluate ecological changes associated with operational modifications by industry, and (4) clarify ecological interactions among the major biotic components of the ecosystem. Several negative impacts of agricultural activities remain including: siltation, rapid drainage due to tiling of fields, and fertilizer and pesticide inputs. This is in part due to the extent of agriculture in this region of North America (Gammon, 1998). Other current impacts to the Wabash River include non-point urban pollution from numerous communities adjacent to the river. Industrial effluents were historically a major source of degradation, which recently appear to have relatively low impact (Gammon, 1998).

However, some unique challenges remain in appraising the dynamic nature of the fish community of the Wabash River. Gammon & Simon (2000) produced an IBI for the Wabash River, and examined variation in this index over a 20-year period. They detected trends in fish diversity and abundances in response to prolonged droughts and floods, and improvements in IBI scores that likely reflected improvements in point source waste treatment. Although the IBI is a suitable index for assessing human disturbance of aquatic systems (Simon, 2003), it was not designed as a tool for discerning other patterns in the fish assemblage. In this study, we combine a multivariate approach with an analysis of the longitudinal river distance gradient based on the species' functional attributes (Poff & Allan, 1995) to examine the fish assemblage of the Wabash River from two years of collections.

Multivariate analyses are exploratory techniques for analyzing species assemblages to find patterns or structure among species and sites, and to test for relationships with environmental variables (Gauch, 1982). In particular, complex data from field surveys can be effectively analyzed using multivariate approaches. The resulting environmental gradient(s) of sites and/or species can then be interpreted using only meaningful variables. Environmental variables are frequently used to explain complexity in fish assemblages at various geographical and temporal scales (Matthews, 1985; Taylor et al., 1993). Large-scale variables include water temperature, and frequency and amount of rainfall. Smaller scale variables focus on variation among local habitats, such as presence and amount of woody debris, local substrata, and presence and quality of the local riparian zone. Relating local habitat features to fish assemblage characterization is the basis of the hypothesis suggested by Gorman & Karr (1978) that stream habitat diversity is related to fish species diversity. Thus, the presence of specific organisms in a stream is directly related to physical and chemical attributes of the stream (Rankin, 1989). Habitat of the stream provides shelter, attachment sites, foraging sites, etc. Intolerant organisms tend to occur in habitats with increased cover, a variety of flows and substrates, low amounts of silt, and low levels of toxic material. More tolerant organisms tend to be associated with slow moving water, tolerate silt, and are more adaptable to a wide range of environmental conditions.

Our first objective was to determine whether variation in the fish assemblage structure in the Wabash River can be explained using several environmental variables in a multivariate analysis. In addition, we tested whether variation in the fish assemblage structure can be explained by the gradient resulting from the multivariate analysis (the hydrological/longitudinal gradient, see below), following Poff & Allan (1995). This approach was used to define fish assemblages in terms of functional similarity and evaluate whether the hydrological regime can explain among-site variation in fish assemblage structure.

Methods

Study area

The Wabash River is the longest river in Indiana with a length of 764 km, and drains an area of 85 500 km^2 (Gammon, 1998). The river flows west and south from its headwaters in Northeast Ohio, across Indiana, and south to the Ohio River confluence (Fig. 1). The Wabash River channel has undergone few modifications, such as channelization or straightening. This lack of modification is likely due to presence of shallows and high flow variation which prevent its use as a navigation channel (Gammon, 1998). The upstream reach of our study area includes distinct riffle–pool sequences during low flows in the summer and has substrata dominated by gravel and cobble. The downstream reach is nearly all run habitat with few distinct riffles and the substratum is dominated by hard clay. A single mainstem reservoir is located on the river at river km 662 although a

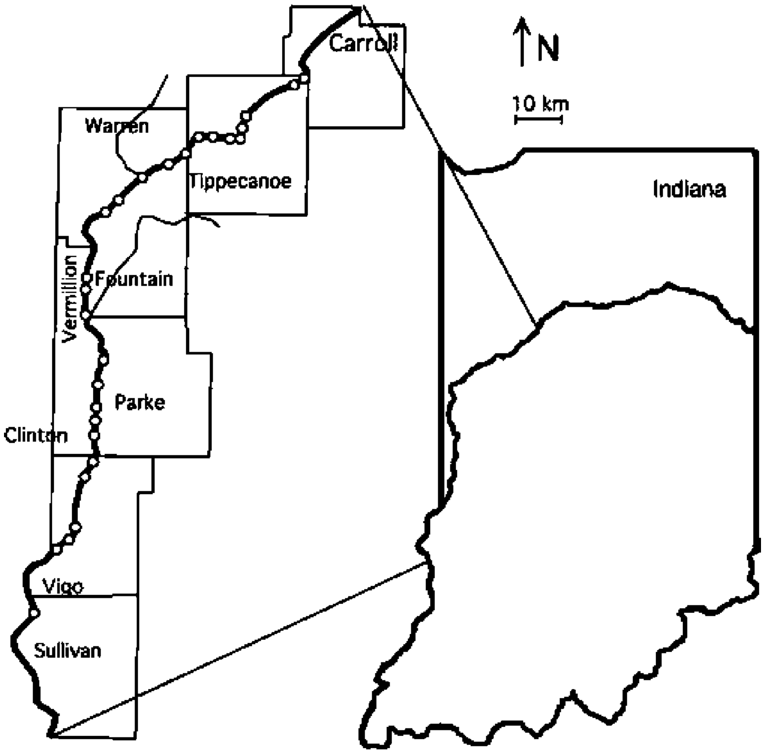

Figure 1. Location of 28 sites on the Wabash River with counties labeled.

number of others are on tributaries (Gammon, 1998). The only major urban areas within our study reach are Lafayette and Terre Haute. Approximately 67% of the watershed is agricultural, primarily row crops (ORSANCO, 1990).

Collection sites and technique

Collection sites and procedures were based on three decades of Wabash River study by Gammon (1998). The 28 sites in this study were 500 m in length and located on outer river bends from river km 530 downstream to river km 300 (Fig.1). All fishes were collected with a boat electrofisher (Smith-Root 5.0 GPP) using DC voltage and two netters. Daytime collections were made three times per summer (late June to mid August) in 2001 and 2002, when river discharge at the Montezuma (United States Geological Survey) gaging station was less than 143 m^3/s (http://waterdata.usgs.gov/in/nwis/current/?type = flow). Individuals greater than 10-cm total length (TL) were identified, TL measured, weighed to the nearest g, and released. Smaller individuals and a subset of all observed species were preserved in 10% formalin and identified or verified later in the laboratory. River sampling reaches were measured using a Garmin III + GPS. Water temperature, dissolved oxygen, pH, and conductivity readings were also recorded at each site using a Hydrolab Quanta portable water quality unit, following fish sampling. Secchi disk readings and other field notes were recorded at this time.

Habitat was evaluated for each site in 2001 using the Qualitative Habitat Evaluation Index (QHEI, Rankin, 1989). This index was developed by the Ohio Environmental Protection Agency to measure physical features of a habitat that affect fish and invertebrate communities. It is based on six metrics (channel geomorphology, riparian zone, substrate, instream cover, pool/riffle development, and stream altitudinal gradient) designed to evaluate a stream's physical environment (Stauffer & Goldstein, 1997). Scoring is based on visual estimates of habitat features by experienced biologists. The metrics are summed for a site score with a maximum value of 100. Undisturbed sites are predicted to result in the highest possible scores, while heavily disturbed sites are expected to receive low scores.

Analyses

Correspondence analysis (CA) is an indirect gradient multivariate technique (Ter Braak & Prentice, 1988) and was used for multivariate analysis. Because rare species tend to have strong impacts on multivariate analyses, and frequently provide results greatly different than when rare species are not included (Ter Braak & Smilauer, 1998), raw data were transformed ($\log x + 1$) to minimize their impact. To further reduce the impact of rare species, only those species with occurrences greater than 100 individuals for combined years total abundance were used in analyses. Correlation coefficients with Bonferroni adjustments were calculated between CA scores and environmental variables. The environmental variables used in the CA included water temperature, pH, dissolved oxygen, conductivity, Secchi depth, river location, QHEI score, and two hydrologic variables: average daily discharge and coefficient of variation (CV) of daily discharge. Average daily discharge data were obtained from USGS gaging station websites for five gaging stations in the same river reach as our 28 sampling sites. Discharge data were available for the past 67 years (average for five sites along the river stretch sampled).

Six functional measures of the fish assemblage (Table 1) were analyzed to determine relationships with the hydrological gradient measured as average daily discharge, following Poff & Allan (1995) but using abundance data (Poff & Allan used presence/absence data). The use of the hydrological/river distance gradient was selected because it was identified as the major gradient from the CA analysis (see below). The proportion of all species falling into subcategories within each functional category was calculated for categorical variables. As an example, the trophic guild category contained eight subcategories. If 10 of 40 species present were omnivores, and 4 species were herbivores, then 0.25 and 0.10 would be entered as the omnivore and herbivore attribute scores for that site. All subcategory scores summed to 1.0. For the two continuous variables (swimming factor and shape factor) the average value for all species present was calculated for each site. For example, the value for swimming factor or shape factor for a site with 20 species was calculated by averaging together the 20 species' values for that attribute (Poff & Allan,

Table 1. Functional measures for fish species taken from Poff & Allan (1995). Correlation coefficients between 25 functional attribute scores (composite score for each fish assemblage) and average daily discharge for 28 sites are listed. Probability values are in parentheses. All categories from Poff & Allen (1995) were not present

Attribute	Discharge *r*
1. Trophic guild	
Herbivore-detritivore	0.277 (0.154)
Omnivore	−0.441 (0.019)
General invertivore	−0.363 (0.058)
Surface/water column invertivore	−0.360 (0.060)
Benthic invertivore	−0.536 (0.003)
Piscivore	−0.270 (0.154)
Planktivore	0.388 (0.079)
2. Stream size preference	
Small and medium streams	−0.413 (0.029)
Medium and large streams	−0.107 (0.587)
Small, medium, and large streams	−0.465 (0.013)
3. Current velocity preference	
Moderate	0.512 (0.005)
Slow-none	0.316 (0.101)
General	0.256 (0.189)
4. Substratum preference	
Rocky, gravel	−0.459 (0.014)
Sand	−0.410 (0.030)
Silt	0.071 (0.721)
General	−0.431 (0.022)
5. Tolerance to silt	
High	−0.045 (0.821)
Moderate	−0.505 (0.006)
Low	−0.439 (0.020)
6. Body morphology	
Swim factor	−0.450 (0.016)
Shape factor	−0.490 (0.008)

1995). These proportions were then all tested for correlations with average daily discharge.

Results

None of the environmental variables had unexpected or high variation (Table 2). Water clarity decreased with downstream distance likely due to increased siltation and increased photosynthesis in downstream reaches. Water temperature increased with downstream distance, although part of this variation was present due to time of day of sampling, and conductivity did not vary with downstream distance. QHEI scores ranged from 30 to 46 – our collection sites had similar habitat scores in part due to the homogeneity of this river reach, and in part due to selection of sites with similar habitat.

Table 2. Means and standard deviations (SD) for environmental variables

Variable	Mean	SD
pH	8.4	0.2
Secchi depth (cm)	33.1	9.4
Dissolved oxygen (mg/l)	10.2	2.2
Conductivity (μmhos)	511	54
Water temperature (°C)	28.1	1.6
QHEI	42	4.5

A total of 68 species was collected during 2001–2002 and the species with highest abundances are ranked in Table 3. The correspondence analysis (CA) explained 31.9, 14.3, and 10.7% of species data variance (eigenvalues = 0.06, 0.02, and 0.02) in the first three axes, respectively. Significant correlates with the first CA axis were average daily discharge, CV of daily discharge, and river location (Table 4). However, no environmental variables were significantly correlated with the 2nd or 3rd CA axes and these axes are not presented. The first axis resulted in a broad distribution of the species (Fig. 2). Five species tended to occur in increased abundances in upstream reaches (*Moxostoma anisurum*, *Moxostoma macrolepidotum*, *Moxostoma carinatum*, *Notropis volucellus*, and *Notropis stramineus*). Species that occurred in higher abundances in downstream reaches included *Micropterus punctulatus*, *Lepisosteus platostomus*, and *Lepomis macrochirus*. The other 17 species tended to occur either in midreaches or to occur throughout the entire sample reach (Fig. 2).

Regressions of average daily discharge on river location and average daily discharge on coefficient of variation of daily discharge resulted in significant linear relationships (Discharge in $m^3/s = -0.99$ * River location in km + 659, $R^2 = 0.94$, $p < 0.01$; CV Discharge in $m^3/s = 0.08$ * Discharge in m^3/s + 63, $R^2 = 0.80$, $p < 0.05$). Coefficient of variation of daily discharge was negatively correlated with river distance (Fig. 3). Based on these

Table 3. Numbers of individuals collected in the Wabash River for species with highest abundances. Abbreviations are for Figure 2

Species	Abbreviation	Abundances
Cyprinella spiloptera Cope	Cspi	2622
Dorosoma cepedianum Lesueur	Dcep	2505
Notropis atherinoides Rafinesque	Nath	2328
Aplodinotus grunniens Rafinesque	Agru	1630
Pimephales vigilax Baird & Girard	Pvig	1243
Notropis blennius Girard	Nble	814
Carpiodes carpio Rafinesque	Ccar	716
Lepomis megalotis Rafinesque	Lmeg	506
Notropis stramineus Cope	Nstr	449
Cyprinus carpio Linnaeus	Cypca	440
Cyprinella whipplei Girard	Cwhi	389
Ictalurus punctatus Valenciennes	Ipun	300
Pylodictis olivaris Rafinesque	Poli	247
Moxostoma macrolepidotum Lesueur	Mmac	226
Pimephales notatus Rafinesque	Pnot	217
Micropterus punctulatus Rafinesque	Mpun	171
Notropis volucellus Cope	Nvol	171
Lepomis macrochirus Rafinesque	Lmac	133
Moxostoma anisurum Rafinesque	Mani	128
Micropterus dolomieu Lacepede	Mdol	125
Moxostoma erythrurum Rafinesque	Mery	124
Ictiobus bubalus Rafinesque	Ibub	101
Lepisosteus osseus Linnaeus	Loss	100
Lepisosteus platostomus Rafinesque	Lpla	96
Moxostoma carinatum Cope	Mcar	66

Table 4. Correlation coefficients for the first CA axis and environmental variables. Bold type refers to significance with Bonferonni correction ($p < 0.05$)

Variable	CA1
pH	0.307
Secchi depth (cm)	0.384
Dissolved oxygen (mg/l)	0.448
Conductivity (μmhos)	0.045
Water temperature (°C)	−0.374
Average daily discharge	**−0.757**
CV daily discharge	**−0.731**
QHEI	0.070
River distance (km)	**0.754**

analyses, river location, average daily discharge, or CV of daily discharge can be used interchangeably to represent hydrologic variation, in further analyses with functional fish attributes. We present further analyses using average daily discharge. River location and CV of daily discharge resulted in nearly identical patterns.

Several of the functional measures of the species (see Poff & Allan, 1995) were related to the hydrologic (distance) gradient (Table 1). Body morphology variables (swimming factor and shape factor) were correlated with the hydrologic (distance) gradient (Table 1). Species with body shapes that are predicted to be better suited for high flow (thin caudal peduncle compared to caudal fin height and fusiform body shape) occurred in higher abundances in locations with lower discharge (upstream reaches with lower CV discharge). Trophic guild classifications were related to the proportion of species at sites from the hydrologic gradient. Species that are omnivores, general invertivores, and benthic invertivores tended to occur in highest proportions at locations with lower discharge (upstream reaches with lower CV discharge). Fish assemblages from these decreased discharge locations had proportionately more species characteristic of medium-large streams and small-large streams. There was no relationship between the hydrologic (distance) gradient and the proportion of species that are characteristic of medium-large streams. Sites with lower daily discharge (upstream reaches with lower CV discharge) had proportionally more moderate-velocity species than downstream sites, while proportions of fishes with general or slow-velocity preferences did not vary with upstream–downstream location. For substratum preference, assemblages at locations with lower daily discharge (upstream reaches with lower CV discharge) had proportionately more species that associate with rocky/gravel and sand substrates. The proportion of species that have low or medium tolerance of silt was higher at sites with lower daily discharge (upstream reaches with lower CV discharge). No patterns were detected between the hydrologic (distance) gradient and the proportion of species that were herbivore–detritivores, surface/water column invertivores, or planktivores. There was no hydrologic (distance) gradient relationship with the proportion of species that prefer silt substrates, and with species that have high tolerance to silt.

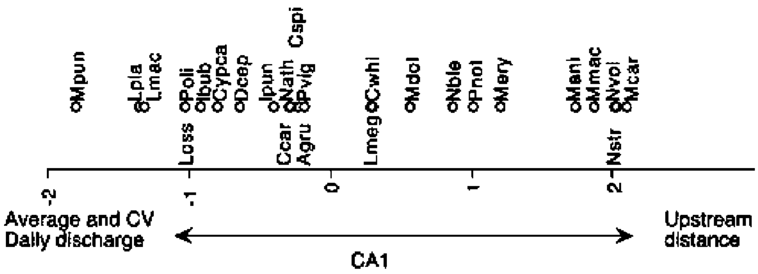

Figure 2. First axis from the correspondence analysis (CA). The 25 species are located on the axis based on highest abundances. Environmental variables that explained the highest variation are listed under the axis. Species abbreviations are in Table 2.

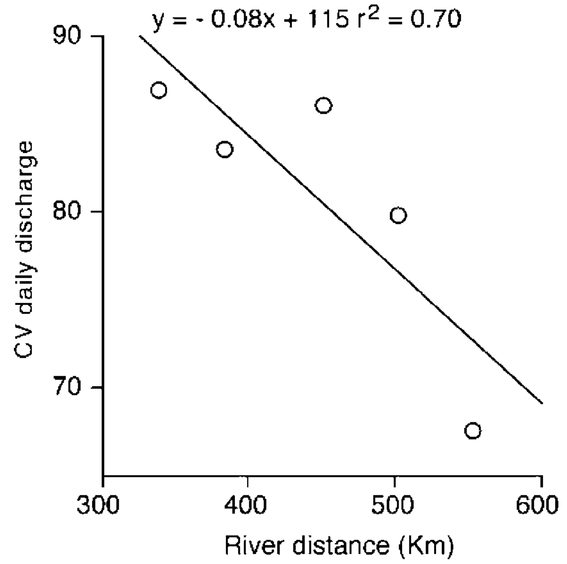

Figure 3. Coefficient of variation of daily discharge and river location for five USGS gaging stations on the Wabash River.

Not surprisingly, combining the species functional measure results with the CA results of the major hydrological variability/distance gradient produced concordant patterns. For example, the *Moxostom*a species and *N. volucellus* have low tolerance to silt and resulted on the right, upstream location, of the ordination (Fig.2). *Lepomis macrochirus, Pylodictis olivaris*, and *Lepisosteus platostomus* are species with high or medium tolerance to silt and occurred on the left, downstream location of the CA ordination (Fig. 2). The *Moxostoma* species prefer streams with rocky or gravel substrates and occurred in highest abundances in upstream locations (Fig. 2). Species that prefer general or silt substrata (e.g., *L. macrochirus*, *P. olivaris*, and *L. platostomus*) occurred in highest abundances in downstream locations (Fig. 2). Species in the central location of the ordination, such as *Pimephales notatus* and *Pimephales vigilax* are general in functional attributes (omnivore trophic guild, general current velocity preference, general substrate preference, and high tolerance to silt). However, not all species in the central location of the ordination (Fig. 2) have these general functional attributes (e.g., *Ictiobus bubalus*, *Aplodinotus grunniens*).

Discussion

Our sample sites on the Wabash River were over a relatively long distance (230 km), resulting in large differences in daily discharge and variation in discharge from upstream to downstream. The hydrological regime in the Wabash River is unlike an unregulated river (Horwitz, 1978; Poff et al., 1997; Resh et al. 1988). In a normal free-flowing stream, upstream reaches have higher variation in discharge than downstream reaches. In contrast, the hydrologic regime of the Wabash River is likely the result of water releases from upstream reservoirs combined with the rapid drainage of rainwater into downstream reaches from agricultural tiling, channelization of downstream tributaries, and urbanization. This altered flow organization likely produces an unnatural disturbance regime, with increased disturbance in downstream reaches and decreased disturbance in upstream reaches (Resh et al., 1988). Further disruption of the downstream habitat has likely occurred as a result of increased sedimentation and alteration of the natural flow regime (Poff et al., 1997). The available habitats to fishes in the Wabash River have changed dramatically during the past century. Gammon (1998) reviewed these changes including decreased water clarity and loss of substrata in downstream reaches.

Fish assemblages at downstream sites (with higher discharge variation) were distinctive from assemblages at upstream sites (with lower discharge variation). Upstream sites were dominated by an assemblage of two minnow species and four redhorse species, while the downstream assemblage was characterized by *L. macrochirus*, two gar species, and *M. punctulatus*. Although many authors have identified longitudinal changes in fish assemblage structure (e.g., Gorman & Karr, 1978; Hughes & Gammon, 1987; Pusey et al., 1995; Peterson & Rabeni, 2001), examinations that include hydrological variation are less frequent (Horwitz, 1978; Bain et al., 1988; Zorn et al., 2002). Herbert & Gelwick (2003) found a pattern of altered fish assemblages in a hydrologically altered southeast Texas stream that was upstream of a reservoir, compared to an unaltered, free-flowing stream. Bain et al. (1988) found that extreme flow variability imposed by a hydroelectric facility on a downstream reach resulted in increased habitat homogeneity and loss of an entire guild of fishes. In the Wabash River, increased flow variability and functional habitat homogeneity appear to influence fish assemblage structure in downstream reaches. Species that are considered to have preferences for moderate current velocity (e.g., *I. bubalus*, redhorse species, and *N. stramineus*) did not occur in higher abundance in downstream reaches, and species with preferences for slow to no current velocity (e.g., *C. carpio*, *L. macrochirus*, and *C. spiloptera*) did not occur in higher abundance in upstream reaches.

Fish species are likely responding to available habitat in the Wabash River. The habitat in the upstream reaches of our study is clearly more suitable to many fish species: the river has a higher gradient (Gammon, 1998), the substrata are more heterogeneous, and water clarity is higher (M. Pyron and T. Lauer, unpubl. data). However, the habitat index we used (QHEI) was not a significant explanatory variable of the fish assemblage. We suggest that this was likely due to low variation in our QHEI scores, based on habitat homogeneity of sites. In addition, our lack of sampling all available habitats at a particular location likely minimized variation among QHEI scores. Our samples typically were located in outer bends of the river, often lacking both shallow pool and riffle habitats. This could easily reduce fish biodiversity based on habitat preferences of some species.

Although anthropogenic impacts including agricultural, industrial, and urban perturbations have dramatically altered the hydrological regime of Midwestern rivers (Karr et al., 1985), the fish assemblage in the Wabash River apparently has responded to these changes. The majority of North American rivers that are similar in size to the Wabash River have experienced greater hydrological alterations, including numerous mainstem dams (Sparks, 1995; Pringle et al., 2000). Although there were no dams present in the 230-km reach that we sampled, additional dams would be predicted to severely disrupt the fish assemblage (Pyron et al., 1998; Quinn & Kwak, 2003).

Poff & Allan (1995) suggested that environmentally variable lotic ecosystems will contain more trophic and habitat generalists than stable ecosystems. In the Wabash River, the fish assemblages from hydrologically variable reaches (downstream) contained fewer species of omnivores, general and benthic invertivores, and piscivores than less hydrologically variable reaches (upstream). Downstream fish assemblages also contained fewer fish species that preferred rocky, gravel, sand, or general substrata, and fewer species with low or medium silt tolerance. Downstream reaches contained fewer species that prefer moderate current and fishes with body morphologies adapted for fast current. Some of these findings were in direct contrast to Poff & Allan (1995). However, their study was over a larger scale that included relatively small streams (largest drainage area = 4092 km^2) and many different fish assemblages, while, our study only included medium to large river sites on a single river (minimum drainage area of 21 700 km^2). In addition, Poff & Allan's study was based on fish presence/absence while we used catch abundance values in our calculations. Differences may have been due to study grain. The scale of our study was the middle stretch of a single river sampled during a two-year period. Poff & Allan (1995) used a dataset of 34 sites in Wisconsin and Minnesota that were collected over several decades. Lastly, the potentially confounding factor of intercorrelation in our study may have influenced the results for the 25 species used in the analysis (Appendix). For example, swim factor was correlated with trophic guild. Our results showed upstream fish assemblages contained more species that were omnivores, general invertivores, and benthic invertivores but their presence may be due to their morphological adaptations (swim factor) for the upstream hydrological regime, rather than feeding preferences. The hydrological pattern that was associated with functional and life-history attributes of the species in this middle section of the Wabash River also resembled predictions from Schlosser (1990). Upstream sites had lower variation (CV) in discharge when compared to downstream sites.

Poff & Allan (1995) suggested that large streams may function like 'headwater' streams if they experience significant seasonal hydrological variability, which may reduce available habitat volume. The hydrological regime of the Wabash River provides evidence to support this hypothesis. For example at the Montezuma gaging station (river 383 km) daily discharge varied from 43 to 1048 m^3/s during 2001 (http://waterdata.usgs.gov/in/nwis/). We found species in downstream reaches with functional attributes that would be predicted for headwater streams (fewer species of omnivores and benthic invertivores). Our results of decreased piscivores, fewer species that prefer fast current, and fewer species with body morphologies for fast current, in downstream reaches may be due to 'low flow bottlenecks' that occur in variable streams where available habitat declines (N. L. Poff, pers. comm.).

The fish assemblage of the Wabash River appears to have recovered from the severe industrial impacts of the past few decades (primarily point source discharges), based on species we collected. Only a few species that were native to the Wabash River have been extirpated (Gammon, 1998), and is in marked contrast to other Midwestern rivers that have lost significant diversity. The Illinois River had lost eight species by the 1980s and the Maumee River had lost 17 species (Karr et al., 1985). Karr et al. (1985) attributed these extirpations to losses of habitats including clear water over clean gravel, but especially to losses of spawning habitats in headwaters, such as well-vegetated marshy areas. Although we did not effectively sample for all species (boat electrofishing is not highly effective at collecting all minnow and darter species), we did find several sensitive species, or species that appear to be recovering from past population declines. This includes, the following species (from Barbour et al., 1999): *Hiodon alosoides* Rafinesque, *Hiodon tergisus* Lesueur, *Erimystax dissimilis* Kirtland, *Hybopsis amblops* Rafinesque, *Nocomis micropogon* Cope, *Cycleptus elongatus* Leseur, *Carpiodes velifer* Rafinesque, and *Moxostoma macrolepidotum*, *M. carinatum*, *M. duquesni* Lesueur, *M. erythrurum*, and *M. anisurum*. Persistence of species in a large watershed such as the Wabash River may be due to the presence of isolated refuges within large watersheds (Karr et al., 1985) when compared to greater species extirpations in smaller watersheds. However, there is little question that the fish assemblage in the Wabash River is extremely different from 100 years ago. Although we do not have historical abundance data, we suggest the following changes likely have occurred to the fish assemblage during the past 100 years. Omnivorous species that are unaffected by increased turbidity (*Dorosoma cepedianum*, *Carpiodes cyprinus*, *Ictiobus cyprinellus*) have likely increased in abundance, as found by Karr et al. (1985) in the Illinois River. Likely decreases in abundance are for visual feeding specialists including top carnivores (e.g., *Alosa chrysochloris* Rafinesque) and invertivore minnows (Karr et al., 1985) such as *Hybopsis amblops* and *Macrhybopsis storeriana* Kirtland. In addition, there has been an increase in abundance of species that rely on olfactory and cutaneous senses such as the catfishes.

One unanswered question is whether our results of the current fish assemblage reflect the native fish assemblage of the Wabash River from prior to human land-use alterations, or if our results are from hydrological modifications from historical and current land-use patterns. Peterson & Kwak (1999) found that similar land-use practices in the Kankakee River basin had a significant effect on the smallmouth bass population. The negative land-use problems that they identified were increased land drainage and urbanization, which resulted in increased flood discharge with sharper peaks and shorter duration (Peterson & Kwak, 1999). The mean annual flow in the Wabash River appears to have increased annually since 1928

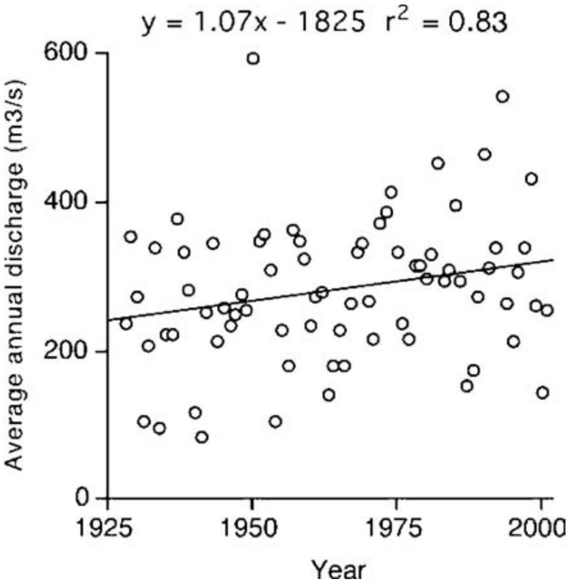

Figure 4. Daily discharge from the USGS gaging station at Montezuma, IN.

(Fig. 4), as in the Kankakee River (Peterson & Kwak, 1999). Herbert & Gelwick (2003) found that the altered hydrology of stream reaches upstream of a reservoir resulted in an increase in tolerant species and a decrease in species richness. In their study, the upstream reaches of the free-flowing stream had higher CV of discharge than the stream reach upstream of a reservoir.

The river distance and hydrological variability gradient in the Wabash River are strongly correlated with the variation in fish assemblages. The gradient is largely due to hydrological changes from upstream to downstream that are concordant with changes in the attributes of species in the fish assemblages. Water temperature, pH, and clarity (Secchi depth) were not significant predictors of variation in the fish assemblage. Additional conservation improvements within the subwatersheds of the Wabash River can result in enhancement of this ecosystem through: (1) modifications of the current regime of rapid drainage of agricultural fields and the resulting hydrologic disruption of the streams; (2) reduced silt and nutrient losses from agriculture; and (3) release of water from reservoirs that more closely mimics a natural flow regime.

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Appendix. Spearman rank correlation matrix for seven functional attribute variables for 25 species. Significant correlation coefficients ($p < 0.05$) are indicated by boldface. WM = water movements, Sub = substrate, SS = stream size, and Tol = silt tolerance

	Swim	Shape	Trophic	WM	Sub	SS	Tol
Swim	1.000						
Shape	0.021	1.000					
Trophic	**0.421**	0.231	1.000				
WM	0.312	0.272	**0.840**	1.000			
Sub	0.375	0.183	**0.931**	**0.768**	1.000		
SS	0.300	0.251	**0.841**	**0.754**	**0.725**	1.000	
Tol	0.300	0.200	**0.933**	**0.845**	**0.877**	**0.796**	1.000