IMPACTS OF PAST GLACIATION EVENTS ON CONTEMPORARY FISH
ASSEMBLAGES OF THE OHIO RIVER BASIN

A THESIS SUBMITTED TO THE GRADUATE SCHOOL IN PARTIAL
FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE MASTER OF
SCIENCE

BY

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BALL STATE UNIVERSITY

MUNCIE, INDIANA

APRIL 2010

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ABSTRACT

THESIS: IMPACTS OF PAST GLACIATION EVENTS ON CONTEMPORARY
FISH ASSEMBLAGES OF THE OHIO RIVER BASIN

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I tested if spatial variation of Ohio River drainage basin fish assemblages, current habitat, water quality, and hydrology were concordant with historic glaciation boundaries.

Assemblage analyses were organized using taxonomic and functional groups.

Multivariate analyses, principal components analysis (PCA) and indicator species analyses, were used to test whether taxonomic and functional assemblages were distinct among regions with varying glacial histories. Principal components analysis was used to identify habitat and water quality as well as hydrologic gradients that could be discerned by glacial region. I identified significant differences in both taxonomic and functional

fish assemblage structure and habitat variation among regions that had different glaciation histories. Recently glaciated Wisconsinan sites were characterized by assemblages of Cyprinidae and Catostomidae families, with high abundances of tolerant fishes that tended to occur in habitats with reduced current velocity. Sites in the Pre-Wisconsinan region were characterized by Cyprinidae, Catostomidae, Centrarchidae, and Percidae families, with increased abundances of intolerant fishes that tended to occur in habitats with coarser substrates and increased water velocity in streams of varying size. Sites in the unglaciated region were dominated by Cyprinidae and Percidae families but were not closely associated with any habitat-based functional group. Taxonomic and functional analyses explained 25% and 40%, respectively, of the variance in assemblage structure. Mean habitat PCA component scores in the unglaciated and Pre-Wisconsinan sites were significantly different than Wisconsinan sites, which were characterized by increased channel structure and reduced stream size. While a multitude of factors impact the distribution of fishes, these results suggest that historical influences such as glaciation may be used to further explain underlying mechanisms of spatial variation in fish assemblages.

Introduction

Variation in stream fish assemblages has traditionally been explained using habitat, anthropogenic influences, and interspecific interactions (Angermeier and Winston 1998). However, potential effects of past glaciation events on contemporary local and regional fish assemblage variation are relatively unknown. Glaciation shaped the landscape of a large portion of the northern hemisphere during the Pleistocene epoch (1.8 million to 10,000 years BP; Black et al. 1973; Flint 1957). During this period, advancing and retreating glaciers moved tremendous amounts of geological surface material thus altering surface topography. Glacial movement also indirectly and directly altered local and regional hydrology through impoundment, diversion, and creation of new drainage pathways. The glacial deposition of till, loess, and alluvium reduced the topography of the entire region, resulting in an overall homogenous terrain (Black et al. 1973; Flint 1957). The outcome was a distinct contrast between the homogenous glaciated regions and the heterogeneous unglaciated landscapes (Black et al. 1973; Flint 1957).

Geographic ranges of fish taxa are products of their evolutionary history and resulting local-scale assemblage variation is strongly influenced by species' distribution boundaries (Ricklefs 1987; Jackson et al 2001). Taxonomic analyses have demonstrated that fish assemblages respond to regional environmental variables and biogeography (Hoeinghaus et al. 2007). Results of taxonomic assemblage analyses are likely due to species turnover (Heino et al. 2007), habitat differences, interspecific interactions, and

dispersal impediments (e.g., dams, abiotic landscapes) that vary across broad geographic ranges (Angermeier and Winston 1998).

Although taxonomic approaches in analyzing assemblages have been successful, an alternative to taxonomic analyses is to group taxa based on functional organization, allowing analyses that discern additional ecosystem information for an assemblage (Poff and Allan 1995). Functional analyses are used to identify assemblage-level variation and have been efficient at detecting ecosystem roles and identifying habitat correlates at local watershed scales (Hoeinghaus et al. 2007; Heino et al. 2007; Pyron et al. in review). Using a functional approach for example, permits comparison of disparate taxonomic assemblages (Poff and Allan 1995). Functional diversity is directly related to ecosystem stability and processes (Tilman 2000).

This study tests whether taxonomic and functional structure of the contemporary fish assemblage varies with historic glacial boundaries. This hypothesis has merit, as genetic differentiation in numerous aquatic species including fishes (Mayden 1988; Berendzen et al. 2003) and invertebrates (Dooh et al. 2006) resulting from the historical presence of glaciers has been shown. Unfortunately, quantifying the direct effects of glaciation on fish assemblages has been difficult (Oberdorff et al. 1995, 1997). Using taxonomic identity and functional groups of habitat preference, trophic guild, tolerance, and body morphology (Poff and Allan 1995) may elucidate some of the legacy of glaciers on contemporary fish assemblages.

The objectives of this study were to: (1) identify whether current taxonomic and functional fish assemblage structure differ with historic glaciation boundaries; (2) to determine whether particular species or functional groups typify glaciated and unglaciated regions; and (3) to test for habitat (Qualitative Habitat Evaluation Index scores, water quality, and physical stream attributes) and hydrologic variation among regions as potential mechanisms to explain current fish assemblage variation within the Ohio, Indiana, and Illinois boundaries of the Ohio River watershed. I hypothesized that differences among glacial regions influenced current fish assemblages and their habitats. This hypothesis has been previously stated, but not tested (Trautman 1981; Jackson and Harvey 1989).

Study area

This study includes the watershed area north of the Ohio River (Ohio, Indiana, and Illinois) that was directly affected by glaciation events and for which fish collections and habitat data were readily available. The area can be separated into three regions based on the influence of the Wisconsinan glaciation events, Pre-Wisconsinan glaciation events, and unglaciated areas (Fig. 1). The entire Ohio River drainage basin is 529,000 km² and has a mean discharge of 8,733 m³/s at the Mississippi River confluence. The basin formed as a result of Pleistocene glaciation (Benke and Cushing 2005) that blocked, diverted, and segmented the ancient Teays River. Portions of the Teays River remain as parts of several of the main tributaries and sections of Ohio River (upper reaches of the Ohio River, Wabash River, and Scioto River). However, much of the current Ohio River mainstem has resulted from recent drainage pathways due to glaciation (Janssen 1953;

Coffey 1961). The result of these events is a difference in the landscapes of the glaciated and unglaciated watersheds. The majority of these effects can be attributed to the recent Wisconsinan and Pre-Wisconsinan (Illinoian) glaciation events. Ice sheet advances prior to the Wisconsinan exceeded the southernmost extent of recent glacial events. Exact locations and definitions of Pre-Wisconsinan era glacial boundaries are similar in overlap and can be attributed to the Illinoian glacial period (Black et al. 1973; Flint 1957).

Methods

Fishes

Stream fish collection data used in this study were obtained by Indiana Department of Environmental Management (IDEM), Ohio Environmental Protection Agency (OEPA), and the Illinois Natural History Survey (INHS) and included sites located in the Ohio River drainage portion of Indiana, Ohio, and Illinois (Fig. 1). Collections were obtained during summer sampling efforts between 1996 and 2007. Collections were made according to agency-based standard assessments using multimetric scoring procedures (e.g., Karr 1981) that can facilitate inter-agency comparisons.

Taxonomic identities were converted into functional groups (Table 1) using the six attributes from Poff and Allan (1995). Two of the variables are continuous (swim and shape factor), and were converted into categorical increments (Table 1) to allow analyses

using relative abundances. Habitat preference information for functional group definitions were from Simon (1999) and Trautman (1981).

A principal components analysis (PCA) was used to reduce variation among fish assemblages by region. Principal components analysis is a multivariate procedure that uses abundance and occurrence simultaneously to detect structure among sites, and weights the strength of this structure through percent variance explained (McCune and Grace 2002). Principal components analysis produces loadings of variables (based on site abundances) that can be used to interpret the direction of gradients and results in a variable-based site characterization. Principal components analysis is robust when quantifying community data using environmental variation, depending on the gradient length (Hirst and Jackson 2007). I used default settings incorporating standardized cross-products matrix correlations for the PCA in PC-ORD (McCune and Mefford 1999). Rare species (occur at fewer than five sites) were eliminated to reduce the effect of outliers (Pyron and Taylor 1993; McCune and Grace 2002). Raw abundance data (taxonomic and functional) were transformed by $\log_{10}(x + 1)$ and PCA axes were interpreted as significant based on stopping rules of the broken stick eigenvalue model, allowing the maximum interpretable variation explained (Jackson 1993). Use of PCA with community assemblage data has been criticized (McCune and Grace 2002; and see discussion by Hirst and Jackson 2007), however, transformation of data, robustness of technique, and comparison of results with other multivariate methods (i.e. identical interpretation of results with detrended correspondence analysis and non metric multidimensional scaling) justify its use. I tested for regional effects of glaciation among the three regions by

comparing the resulting mean PCA axis scores with one-way analysis of variance (ANOVA) and post hoc Tukey (95% CI) comparisons. The regions were defined as a Wisconsinan glaciated area, a Pre-Wisconsinan glaciated area, and an unglaciated area (Fig. 1). Sample sizes for analyses of taxonomic identities and functional groups differed because of the rarity definition (functional groups had different membership, the deletion of rare groups differed from the taxonomic data). The α level for all tests was 0.05.

I used indicator species analysis (ISA, Dufrene and Legendre 1997) in PC-ORD to identify species and functional groups that best discerned Wisconsinan, Pre-Wisconsinan, and unglaciated regions. Indicator species analysis measures the relative abundance and exclusivity of a particular species or functional group in a region. The ISA was used to supplement the PCA as an additional measure of taxonomic and functional group distinction among *a priori* selected study regions (McCune and Grace 2002). Species indicator values range from 100 for a perfect regional indicator, to 0 for a poor regional indicator. Significances of species indicator values were obtained from Monte Carlo simulations with 5000 randomizations.

Habitat and water quality

I used IDEM habitat and water quality parameters that were only available for Indiana sites. Indiana Department of Environmental Management habitat data were QHEI (Rankin, Ohio EPA 1989) metrics, water quality variables, and continuous physical measurements. QHEI habitat parameters included individual metric scores or percentages for substrate coarseness, instream cover, canopy cover, channel development, riparian

zone structure, pool, glide, and riffle run development, and stream gradient. Water quality variables were dissolved oxygen, pH, water temperature, specific conductivity, and turbidity. Continuous physical measurements were stream width (mean), water depth (max and mean), and drainage area. I used a PCA to reduce the habitat and water quality variables into several new uncorrelated axes. Resulting PCA axes were interpreted using the broken stick eigenvalue model (Jackson 1993) and mean scores were compared by region using one-way ANOVAs and Tukey tests (95% CI).

I used daily discharge data from 41 USGS gaging stations in the study region for hydrologic analyses (<http://waterdata.usgs.gov/>). The mean range of gaging station records from these sites was 78 years. Gaging stations were selected by geologic region (14 unglaciated, 10 Pre-Wisconsinan, 17 Wisconsinan) with the assumption that these stations were representative for fish collection sites. Daily discharge data were analyzed using the Indicators of Hydrologic Alteration flow-based software (IHA, The Nature Conservancy, 2006; Richter et al. 1996). IHA software calculates ecologically relevant hydrologic variables from daily discharge that allows detection of significant alterations in flow regime for a time period. The IHA software produces 33 hydrologic variables in five categories: magnitude of monthly water conditions, magnitude and duration of annual extreme water conditions, timing of annual extreme water conditions, frequency and duration of high and low pulses, and rate and frequency of water condition changes. I used IHA to calculate significantly altered hydrologic variables for each gaging station, by using regressions of hydrology variables against year. Frequencies of significantly altered hydrologic variables were interpreted through R^2 values and significant p-values

(see discussion by Richter et al. 1996) and condensed into PCA axes which were interpreted using the broken stick model (Jackson 1993). Mean PCA site scores were compared among the three regions using one-way ANOVA and Tukey (95% CI) comparisons.

Results

The collections included 3,524,200 individuals of 154 species (Appendix 1). Taxonomic analyses included 3,119 Wisconsinan, 725 Pre-Wisconsinan, and 1,358 unglaciated sites, and functional analyses included 3,179 Wisconsinan, 735 Pre-Wisconsinan, and 1,416 unglaciated sites. The species with highest abundances were central stoneroller (*Campostoma anomalum*), creek chub (*Semotilus atromaculatus*), bluntnose minnow (*Pimephales notatus*), western blacknose dace (*Rhinichthys obtusus*), and striped shiner (*Luxilus chrysocephalus*). The least abundant species included lake chubsucker (*Erimyzon sucetta*), cypress darter (*Etheostoma proeliare*), spotted gar (*Lepisosteus oculatus*), silver carp (*Hypophthalmichthys molitrix*), and shovelnose sturgeon (*Scaphirhynchus platyrhynchus*). The Wisconsinan region had highest occurrences (percentage of sites) of bluntnose minnow (84 %), creek chub (80 %), green sunfish (*Lepomis cyanellus*, 79 %), white sucker (*Catostomus commersonii*, 74 %), and central stoneroller (73 %). The Pre-Wisconsinan region had highest occurrences (percentage of sites) of bluntnose minnow (85 %), bluegill (*Lepomis macrochirus*, 74 %), central stoneroller (73 %), green sunfish (70 %), and longear sunfish (*Lepomis macrolepidotum*, 65 %). The unglaciated region had highest occurrences (percentage of

sites) of bluntnose minnow (78 %), creek chub (78 %), central stoneroller (70 %), green sunfish (70 %), and johnny darter (*Etheostoma nigrum*, 64 %).

Taxonomic assemblage structure

Five PCA axes of taxonomic identities were significantly different than random and accounted for 25% of the total taxonomic assemblage variation (Table 2). The first PCA axis (Fig. 2; eigenvalue 13.6) accounted for 9.1% of the variance. There were significant differences for mean PCA1 site scores among regions, indicating differences in assemblages by region (Table 3). Tukey comparisons resulted in mean PCA scores for the Wisconsin region that were significantly higher than scores for the unglaciated region, which were significantly higher than scores for the Pre-Wisconsinan region. Freshwater drum (*Aplodinotus grunniens*), channel catfish (*Ictalurus punctatus*), smallmouth buffalo (*Ictiobus bubalus*), longnose gar (*Lepisosteus osseus*), river carpsucker (*Carpionodes carpio*), flathead catfish (*Pylodictus olivaris*), and spotfin shiner (*Cyprinella spiloptera*) had high negative loadings on PCA1 consistent with Pre-Wisconsinan sites (Table 2). Fishes that had high positive loadings on PCA1 were creek chub, western blacknose dace, and white sucker and were representative of Wisconsin sites (Table 2).

The second PCA axis (Fig. 2; eigenvalue 8.7) of taxonomic identity accounted for 5.8% of the variance. Mean PCA2 scores based on taxonomic assemblages were significantly different by region (Table 3). Tukey comparisons were significant such that mean PCA scores for sites in unglaciated regions were higher than Wisconsin, and

mean scores for the Pre-Wisconsinan region were not significantly different from than the unglaciated or Wisconsinan. The fishes with high negative loadings on PCA2 were greenside darter (*Etheostoma blennioides*), northern hog sucker (*Hypentelium nigricans*), central stoneroller, rainbow darter (*Etheostoma caeruleum*), and striped shiner (Table 2) and were consistent with Wisconsinan and Pre-Wisconsinan sites. Fishes with positive loadings on PCA2 included smallmouth buffalo, river carpsucker, freshwater drum, and flathead catfish (Table 2) and were consistent with unglaciated sites.

The third taxonomic PCA axis (eigenvalue 4.9) accounted for 3.3% of the variance (Table 2). Mean scores for the third PCA axis of taxonomic assemblages were significantly different by region (Table 3). Tukey comparisons resulted in significantly higher PCA means for unglaciated and Pre-Wisconsinan areas compared to the Wisconsinan region. Fishes that loaded negatively on this PCA axis were bluegill, warmouth (*Lepomis gulosus*), largemouth bass (*Micropterus salmoides*), carp (*Cyprinus carpio*), white crappie (*Pomoxis annularis*), and black crappie (*Pomoxis nigromaculatus*) (Table 2) and were consistent with Wisconsinan sites. Fishes that had positive loadings on this axis included central stoneroller, fantail darter (*Etheostoma flabellare*), emerald shiner (*Notropis atherinoides*), creek chub, and western blacknose dace (Table 2) and were consistent with unglaciated and Pre-Wisconsinan sites.

The fourth taxonomic PCA axis (eigenvalue 3.8) accounted for 2.5% of the variance (Table 2). Mean fourth PCA axis scores of taxonomic assemblages were significantly different among regions (Table 3). Tukey comparisons were significant with

mean Pre-Wisconsinan PCA scores higher than unglaciated region scores, which were higher than mean Wisconsinan scores. Fishes that had high negative loadings were white sucker, largemouth bass, bluegill, green sunfish, and white crappie (Table 2) and were consistent with Wisconsinan sites. Fishes that had high positive loadings were pirate perch (*Aphredoderus sayanus*), slough darter (*Etheostoma gracile*), western mosquitofish (*Gambusia affinis*), and ribbon shiner (*Lythrurus fumeus*) (Table 2) and were consistent with Pre-Wisconsinan sites.

The fifth PCA axis (eigenvalue 3.6) accounted for 2.4% of the variance (Table 2). Mean fifth PCA axis scores of taxonomic assemblages were significantly different among regions (Table 3). A Tukey comparison resulted in mean Pre-Wisconsinan PCA scores significantly higher than the unglaciated scores, which were higher than, mean scores in the Wisconsinan region. Fishes that had high negative loadings were bluebreast darter (*Etheostoma camurum*), streamline chub (*Erimystax dissimilis*), and river chub (*Nocomis micropogon*) (Table 2) and were consistent with Wisconsinan sites. Fishes with high positive loadings were bluntnose minnow, johnny darter, and green sunfish (Table 2) and were consistent with Pre-Wisconsinan sites.

Functional assemblage structure

The functional PCA resulted in two significant axes that accounted for 55% of the total variance among assemblages (Fig. 3; Table 4). The first and second PCA axes separated assemblages based on habitat preferences, morphological characters, silt tolerance, and trophic functional attributes. The first PCA axis (Fig 3; eigenvalue 17.2)

accounted for 40% of the variation based largely on trophic group membership and body morphology (Table 4). Mean first PCA axis scores for functional groups were significantly different among regions (Table 3). A Tukey comparison resulted in mean Pre-Wisconsinan scores that were significantly different from Wisconsinan scores, which were higher than mean unglaciated region scores. The functional groups with highest loadings on PCA1 were categories of moderately intolerant to silt, intermediate shape and swim factor, and general substrate and stream size preferences (medium-large stream / lentic) (Table 4) and were consistent with Pre-Wisconsinan sites.

The second functional PCA axis (Fig. 3; eigenvalue 5.6) explained 13% of the assemblage variation based on functional groups of habitat preference, morphological characters, and trophic functional groups. Mean second PCA axis scores for functional groups were significantly different among regions (Table 3). A Tukey comparison resulted in significantly higher mean Pre-Wisconsinan PCA scores than Wisconsinan and unglaciated scores. Functional groups with negative loadings on PCA2 were moderate level swim factor shapes (SwF 0.35-0.45, SwF 0.55-0.65), general trophic groups of omnivore and herbivore, high tolerance to silt, and preferences for lentic stream size, increased current velocity, substrate coarseness, and decreased stream size (Table 4) and were consistent with unglaciated and Wisconsinan sites. Attributes with positive loadings on PCA2 were low and high extremes in shape factor (ShF 1.5-2.5, ShF 2.5-3.5, ShF 3.5-4.5, and ShF 12.5-13.5), specialized trophic groups (piscivorous and planktivorous), and preferences for lotic stream size, decreased current velocity, decreased substrate

coarseness, and increased stream size (Table 4) and were consistent with Pre-Wisconsinan sites.

Indicator species analyses

Indicator species analysis resulted in 26 species that best typified the study regions (Table 5). The analysis resulted in a distinct Pre-Wisconsinan group of taxonomic and habitat specialists. The unglaciated and Wisconsinan regions had six significant indicator species and 14 species were indicators for the Pre-Wisconsinan region. Highest indicator species (top 10) included green sunfish and white sucker in the Wisconsinan region; longear sunfish, central stoneroller, spotfin shiner, bluegill, and greenside darter in the Pre-Wisconsinan region; and creek chub, fantail darter, and johnny darter in the unglaciated region. Indicator species analysis resulted in 27 functional groups that were significant indicators for study regions (Table 6). The Pre-Wisconsinan region was best described by 25 functional groups, the Wisconsinan by two, and the unglaciated region was not significantly represented by any functional groups. The highest indicator functional groups (top 10) included small-large stream, sand substrate, low-medium tolerance, general and benthic invertivore, herbivore, slow current, and moderate shape and swim factor habitat specialist that categorized one region (Pre-Wisconsinan).

Habitat, water quality, and hydrology

Habitat and water quality analyses used data from 935 sites in Indiana. The habitat and water quality PCA resulted in two significant axes (Fig. 4; Table 7) that accounted for 35% of the total variation in QHEI metrics and water quality variables. The

first PCA axis (eigenvalue 4.2; Fig. 4) explained 19% of the variance among sites. Mean PCA1 scores were significantly different among regions (Table 3) and a Tukey comparison showed significantly higher mean PCA scores for unglaciated and Pre-Wisconsinan regions than mean PCA scores for the Wisconsinan region. Variables that loaded negatively on PCA1 were channel structure, percent riffle, and substrate type (low coarseness) (Table 7) and were consistent with Wisconsinan sites. Drainage area, mean stream width, and water depth (mean and maximum) had positive loadings on PCA1 (Table 7) and were consistent with unglaciated and Pre-Wisconsinan sites.

The second habitat PCA axis (eigenvalue 3.5; Fig. 4) explained 16% of the variance among sites. Mean scores for PCA2 of habitat and water quality were significantly different among regions (Table 3) and a Tukey comparison showed significantly lower mean scores in unglaciated and Pre-Wisconsinan regions than the Wisconsinan region. Water depth (mean and max), stream width, drainage area, and stream cover had high negative loadings on PCA2 (Table 7) and were consistent with unglaciated and Pre-Wisconsinan sites. Stream gradient loaded positively on PCA2 (Table 7) and was consistent with Wisconsinan sites.

The separate PCA analysis of hydrology data condensed results from the indicators of hydrologic alteration (IHA) analysis. The IHA analysis resulted in significant hydrologic alterations for all 41 gaging stations, and the resulting first PCA axis was significant according to the broken stick model (Table 8). The first PCA axis resulted in high negative loadings for four (of five) IHA parameter groups of magnitude

of monthly water conditions, magnitude and duration of annual extreme water conditions, frequency and duration of high and low pulses, and rate/frequency of water condition changes. However, an ANOVA of mean first PCA axis scores for hydrologic alterations did not result in any significant differences among glacial study regions (Table 3).

Discussion

Inferences based on glacial boundaries

Aquatic assemblages are considered to be a product of historical biogeography and hierarchical scales of regional and local environmental gradients (Jackson et al. 2001). My analyses indicated that taxonomic and functional fish assemblages differ among regions that have different timing of glaciation events. Concordant habitat variation provides additional support for assemblage differences among glaciation regions. Jacquemin and Pyron (*in review*) found that Indiana fish assemblages (taxonomic and functional) were highly correlated ($r > 0.7$) with habitat and water quality parameters. These multiple levels of environmental (habitat) complexity contribute to, and support diverse fish assemblage structure (Matthews 1998; Angermeier and Winston 1998). When a major environmental impact like glaciation occurs, the landscape and associated habitats are disrupted and restructured at all scales.

Separating historical effects from contemporary ecological impacts on fish assemblages tends to be complex and is inherently difficult to quantify (Endler 1982). Historical influences may be diluted through widespread basin homogenization including

habitat fragmentation, hydrologic alterations, species extirpations or introductions of exotics, and other anthropogenic influences (Olden and Poff 2004). An additional complication is that anthropogenic activities and natural gradients tend to be correlated (Allan 2004). Separation of natural and anthropogenic gradients that are correlated has been difficult or impossible in watershed analyses (Allan 2004; Yates and Bailey 2010). In the Ohio River watershed, the relationship between anthropogenic environmental impacts such as agricultural land use and glacial boundaries, is primarily caused by variation in soil and topography. Glaciation events produced low topographical relief through soil deposition in glaciated landscapes compared to unglaciated regions (Black et al. 1973; Flint 1957), resulting in increased agricultural land use in glaciated regions. Land use in the glaciated Wisconsin region of Indiana is approximately 89% agricultural (calculated from 1992 USGS Land Cover Survey; <http://inmap.indiana.edu/>). However, the Pre-Wisconsinan and unglaciated regions of Indiana have 55% and 50% agricultural land use, respectively. Watersheds in Wisconsin that have similar agricultural impacts as in the Ohio River basin had strong fish assemblage effects that were only detected when agricultural land use was higher than 50% (Wang et al. 2003). Application of the 50% threshold to the Ohio River basin would imply fish assemblage effects throughout the entire study region. In addition, hydrologic alterations that result from anthropogenic influences further complicate assemblage analyses. In an analysis of hydrologic alterations among glaciation regions, I found no differences in the frequencies of significantly altered hydrology variables between glaciated regions. All of these Ohio River subwatersheds have similar agricultural and hydrologic impacts. My interpretation is that while agricultural and hydrological alterations negatively impact fish assemblages

(Yates and Bailey 2010), the influence of past glaciation history provides an additional detectable signal, that can be recognized as a contributing factor to assemblage variation.

Taxonomic and functional assemblage comparisons

My analyses of taxonomic and functional based assemblages indicated significant assemblage structure that is related to environmental gradients. Variation in fish assemblages among the Indiana reaches of the Ohio River basin are a function of habitat heterogeneity (Jacquemin and Pyron in review). My results for taxonomic analyses were largely based on species abundance variation with stream size, flow, and silt, while functional groups analyses resulted in abundance variation with microhabitat preferences, body morphology, silt tolerance, and trophic group.

Functional analyses condense individual taxa into guilds, which respond to environmental variation stronger than individual taxa (Austen 1994). Functional analyses explained a larger component of assemblage variation (30% more) and resulted in higher indicator values than taxonomic-based analyses. Analyses using functional groups are expected to differ from analyses using taxonomic identities. However, my results did not support the predictions of Hoeinghaus et al. (2007), who found a stronger taxonomic-based response to regional environmental variation than for functional groups. Hoeinghaus et al. (2007) found that functional groups had stronger relationships with local environmental variation. This may result from physiographic differences among study regions, or a lack of species turnover (Heino et al. 2007) resulting in higher beta diversity among Texas river basins than among basins in the Ohio River drainage. My

analysis demonstrated that functional groups best explained regional environmental variation in the Ohio River basin. This suggests the presence of habitat variation across the basin.

Despite differences in current land use (i.e. presence and degree of agricultural regimes), the geologic features of the three regions appear to be distinct and to control habitat variation and the associated fish assemblages. Taxonomic and functional assemblages were consistently different by geologic region. Indicator species analysis resulted in a Pre-Wisconsinan assemblage that had the strongest functional group and taxonomic membership. The habitat analysis also resulted in differences among glaciated regions. Habitat variation is the likely mechanism for producing subsequent variation in fish assemblages (Jackson et al. 2001), including a distinct Pre Wisconsinan assemblage. This may be a product of an intermediate area that was not subject to the most recent glaciation event but which was affected by prior glacial disturbance events. This Pre Wisconsinan location is characterized by intermediate topography and till depths, and different anthropogenic (e.g. land use) influences than the concentrated agricultural practices that occur in the Wisconsinan region (Black et al. 1973; Flint 1957). Patterns of anthropogenic use largely result from glacial history, resulting in recent disturbance regimes that continue to influence these aquatic ecosystems.

Integration of community ecology, systematics, and historical biogeography

Traditional biogeographical techniques of explaining biotic occurrence patterns have focused on the systematics and evolution of taxa from vicariance events (Mayden

1988; Wiens and Donoghue 2004). My results are novel, as few studies examine community variation that can be explained by historical biogeography (Oberdorff et al. 1997). During glaciation events the Mississippi River and smaller tributaries provided refugia to fishes. Subsequent dispersal from these refugia during post-glacial periods likely resulted in species assembly based on tributary connections (Oberdorff et al. 1997). Refugia such as these provided a bank of species for recolonization following glacial retreat and exposed taxa to newly formed habitats and allowed subsequent building of new assemblages. Combining phylogenetic studies with historical events may provide further insight on the influences of dispersal, speciation, and trait distribution on assemblage variation (Ingram and Shurin 2009).

My results show contemporary Ohio River basin fish assemblages that retain the vast majority of historical taxa but have variation in organization due to multiple disturbances. Although there were apparently relatively few extinction events in the basin as a result of glaciation (Oberdorff et al. 1997), fish assemblage structure was altered by glacial impacts. Historic species retentions suggest that community assemblage following glaciation occurred by dispersal and not through adaptive radiation, implying trait and niche conservatism (Wiens and Donoghue 2004; Cavender-Bares et al. 2009). Understanding of spatial abiotic gradients provides insight into temporal variation and potential mechanisms for the observed structure of assemblages.

Conclusion

Historical processes such as glaciation can be tested as spatial contributors that influence current fish assemblage structure. In Ohio River basin fish assemblages, large scale environmental variation correlated with glacial boundaries was best identified from a functional approach in contrast to a taxonomic approach. An increase in variation explained by functional groups coupled with abiotic variation of streams in the study area suggests a relatively high degree of habitat specialization in the fishes. Contemporary stream habitats can be seen as a by-product of glaciation history and current land use. My study discerned a difference in fish assemblages according to spatial geologic variability. Incorporating historical events into analyses of fish assemblages and habitat variation is a powerful approach that can contribute to our understanding of community ecology.

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Table 1. Functional attributes of fishes used in the analysis separating unglaciated, Pre-Wisconsinan, and Wisconsinan regions (Poff and Allan 1995). Body morphology variables were converted from continuous numbers into discrete categories for analysis.

Functional Measure	Subcategory
Trophic guild	Herbivore-detritivore Omnivore General invertivore Surface/water column invertivore Benthic invertivore Piscivore Planktivore Parasite
Habitat classification	
Stream size preference	Small and medium streams Medium and large streams Small, medium, and large streams Lentic
Current velocity preference	Fast Moderate Slow-none General
Substratum preference	Rubble (rocky, gravel) Sand Silt General
Tolerance	High Medium Low
Body Morphology	
Swimming factor	0.15-0.25 0.25-0.35 0.35-0.45 0.45-0.55 0.55-0.65 0.65-0.75 0.75-0.85 0.85-0.95
Shape factor	0.0-1.5 1.5-2.5

2.5-3.5
3.5-4.5
4.5-5.5
5.5-6.5
6.5-7.5
7.5-8.5
8.5-9.5
9.5-10.5
10.5-11.5
11.5-12.5
12.5-13.5
13.5-14.5

Table 2. Highest loadings for fish species from taxonomy-based principal component analysis of glaciated regions.

Species	PC 1	Species	PC 2	Species	PC 3	Species	PC 4	Species	PC 5
	-		-		-		-		-
Freshwater drum	0.20	Greenside darter	0.25	Bluegill	0.22	White sucker	0.23	Streamline chub	0.16
Channel catfish	-0.20	N. hogsucker	-0.23	Pumpkinseed	-0.21	Largemouth bass	-0.20	River chub	-0.15
Spotfin shiner	-0.19	Striped shiner	-0.23	Largemouth bass	-0.21	W. blacknose dace	-0.17	Bluebreast darter	-0.14
Golden redhorse	-0.18	Rock bass	-0.23	White crappie	-0.19	Creek chub	-0.17	Black redhorse	-0.14
River carpsucker	-0.18	Rainbow darter	-0.22	Yellow perch	-0.18	Bluegill	-0.17	Rosyface shiner	-0.13
								Smallmouth	
Golden shiner	-0.17	Central stoneroller	-0.21	Common carp	-0.18	Pumpkinseed	-0.16	redhorse	-0.12
Smallmouth		Bluntnose							
buffalo	-0.17	minnow	-0.21	Black crappie	-0.18	Green sunfish	-0.15	Variegate darter	-0.11
Emerald shiner	-0.17	Banded darter	-0.20	Warmouth	-0.17	White crappie	-0.14	Silver redhorse	-0.09
Silver redhorse	-0.17	Silver shiner	-0.19	Goldeye	-0.16	Common shiner	-0.14	Tippecanoe darter	-0.09
Flathead catfish	-0.17	Smallmouth bass	-0.18	Green sunfish	-0.15	Common carp	-0.14	River redhorse	-0.09
Silverjaw minnow	0.04	White bass	0.07	Silverjaw minnow	0.12	Pugnose minnow	0.11	Mud darter	0.15
						Blackstripe			
Fathead minnow	0.04	Flathead catfish	0.08	Rainbow darter	0.12	topminnow	0.12	Bullhead minnow	0.15
				Smallmouth		Blackspotted		Miss. silvery	
Fantail darter	0.05	Bigmouth buffalo	0.08	buffalo	0.12	topminnow	0.12	minnow	0.16
Mottled sculpin	0.05	Skipjack herring	0.08	Bullhead minnow	0.12	Miss. silvery minnow	0.13	Green sunfish	0.16
Orangethroat									
darter	0.06	Emerald shiner	0.09	Emerald shiner	0.12	Pirate perch	0.14	Longear sunfish	0.17
Johnny darter	0.07	Black buffalo	0.10	Fantail darter	0.13	Bluntnose darter	0.16	Blackside darter	0.18
S. redbelly dace	0.08	Freshwater drum	0.10	S. redbelly dace	0.15	Mosquito fish	0.17	Redfin shiner	0.19
White sucker	0.10	River carpsucker	0.11	Creek chub	0.18	Mud darter	0.17	Silverjaw minnow	0.19
W. blacknose dace	0.12	Bullhead minnow	0.12	Central stoneroller	0.19	Ribbon shiner	0.17	Johnny darter	0.21
Creek chub	0.17	Smallmouth	0.13	W. blacknose dace	0.20	Slough darter	0.18	Bluntnose minnow	0.22
		buffalo							

Table 3. Results of one way analysis of variance by Wisconsinan, Pre-Wisconsinan, and unglaciated regions.

Source of variation	ss	df	MS	<i>F</i>	<i>P</i>
Taxonomic assemblage					
PCA 1					
Among regions	2278.8	2	1139.4	86.6	< 0.001
Error	68425	5199	13.2		
PCA 2					
Among regions	98.14	2	49.07	5.65	< 0.004
Error	45193	5199	8.69		
PCA 3					
Among regions	466.8	2	233.4	48.33	< 0.001
Error	25106	5199	4.83		
PCA 4					
Among regions	466.1	2	233.1	62.8	< 0.001
Error	19303	5199	3.7		
PCA 5					
Among regions	342.2	2	171.1	48.8	< 0.001
Error	18222	5199	3.5		
Functional assemblage					
PCA 1					
Among regions	645.6	2	322.8	18.91	< 0.001
Error	90933	5327	17.1		
PCA 2					
Among regions	556.4	2	278.2	50.77	< 0.001
Error	29192	5327	5.48		
Habitat					
PCA 1					
Among regions	277.7	2	138.9	35.2	< 0.001
Error	3676	932	3.9		
PCA 2					
Among regions	151.5	2	75.7	22.6	< 0.001
Error	3121	932	3.4		
Hydrology					
PCA 1					
Among regions	0.7	2	0.3	0.1	0.87
Error	95.1	40	2.4		

Table 4. Loadings from principal component analysis of functional groups.

Functional Group	PC 1	Functional Group	PC 2
Swim factor (0.15-0.25)	0.00	Small stream	-0.32
Shape factor (11.5-12.5)	0.00	Omnivore	-0.22
Swim factor (0.85-0.95)	0.00	Rubble (rocky, gravel) substratum	-0.22
Shape factor (9.5-10.5)	0.00	Moderate current	-0.20
Parasite	0.01	Herbivore-detritivore	-0.18
Shape factor (8.5-9.5)	0.02	Fast current	-0.17
Shape factor (13.5-14.5)	0.03	General current	-0.15
Shape factor (12.5-13.5)	0.04	Swim factor (0.35-0.45)	-0.12
Shape factor (7.5-8.5)	0.05	High tolerance	-0.11
Swim factor (0.65-0.75)	0.06	Swim factor (0.55-0.65)	-0.10
Medium-large stream	0.20	Slow-absent current	0.15
Low tolerance	0.20	Shape factor (12.5-13.5)	0.17
Swim factor (0.35-0.45)	0.20	Small-large stream	0.19
Lentic	0.20	Shape factor (1.5-2.5)	0.21
Benthic invertivore	0.21	Surface/water column invertivore	0.22
Swim factor (0.45-0.55)	0.21	Piscivore	0.23
Shape factor (5.5-6.5)	0.21	Shape factor (3.5-4.5)	0.23
Medium tolerance	0.21	Silt substratum	0.25
General substratum	0.21	Planktivore	0.27
Shape factor (4.5-5.5)	0.21	Shape factor (2.5-3.5)	0.27

Table 5. Significant fish taxa from taxonomy-based indicator species analysis by Wisconsinan, Pre-Wisconsinan, and unglaciated region.

Species	Region	Indicator Value (IV)	Mean Random
Longear sunfish	Pre Wisconsinan	36.5	14.9
Green sunfish	Wisconsinan	34.3	26.4
Creek chub	Unglaciaded	33.6	26.9
Central stoneroller	Pre Wisconsinan	32.4	25.8
White sucker	Wisconsinan	31.3	24.2
Spotfin shiner	Pre Wisconsinan	27.6	14.7
Bluegill	Pre Wisconsinan	27.6	23.1
Fantail darter	Unglaciaded	25.7	15.9
Johnny darter	Unglaciaded	25.4	21.3
Greenside darter	Pre Wisconsinan	24.9	18
N. hogsucker	Pre Wisconsinan	24.9	18.6
Rainbow darter	Pre Wisconsinan	23.9	16.8
Striped shiner	Unglaciaded	22.3	19.4
Carp	Wisconsinan	21.8	12.9
Smallmouth bass	Pre Wisconsinan	21.2	13.2
Largemouth bass	Wisconsinan	21.0	15.7
W. blacknose dace	Wisconsinan	20.9	15.4
Golden shiner	Pre Wisconsinan	20.2	13.2
Sand shiner	Pre Wisconsinan	20.1	13.3
Logperch	Pre Wisconsinan	19.4	10.5
Silverjaw minnow	Pre Wisconsinan	18.4	14.6
Rock bass	Pre Wisconsinan	17.7	15.3
Spotted bass	Pre Wisconsinan	16.7	7.8
Fathead minnow	Wisconsinan	16.5	5.8
S. redbelly dace	Unglaciaded	14.9	5.9
Blackside darter	Unglaciaded	14.7	5.2

Table 6. Significant functional groups from indicator species analysis by Wisconsinan, Pre-Wisconsinan, and unglaciated region.

Functional Group	Region	Indicator Value (IV)	Mean Random
Small-large stream	Pre Wisconsinan	42.0	28
Sand substratum	Pre Wisconsinan	40.9	29.1
Medium tolerance	Pre Wisconsinan	40.5	33.2
General invertivore	Pre Wisconsinan	40.3	31.7
Herbivore-detritivore	Pre Wisconsinan	38.5	27.5
Swim factor (0.55-0.65)	Pre Wisconsinan	37.9	30.6
Low tolerance	Pre Wisconsinan	37.7	31.5
Shape factor (4.5-5.5)	Pre Wisconsinan	37.5	33
Benthic invertivore	Pre Wisconsinan	37.3	32.1
Slow-absent current	Pre Wisconsinan	37.1	32.9
Moderate current	Pre Wisconsinan	37.0	33.5
Swim factor (0.35-0.45)	Pre Wisconsinan	36.9	33.7
Medium-large stream	Pre Wisconsinan	36.8	29.6
Shape factor (5.5-6.5)	Pre Wisconsinan	36.4	32
Swim factor (0.45-0.55)	Pre Wisconsinan	36.1	33.3
Lentic	Wisconsinan	35.9	33.3
Shape factor (3.5-4.5)	Pre Wisconsinan	35.8	30.1
Rubble (rocky, gravel) substratum	Pre Wisconsinan	35.8	33.4
Shape factor (2.5-3.5)	Pre Wisconsinan	35.2	29.4
High tolerance	Wisconsinan	34.9	33.6
Shape factor (1.5-2.5)	Pre Wisconsinan	34.7	25.5
General substratum	Pre Wisconsinan	34.6	33.1
Surface/water column invertivore	Pre Wisconsinan	32.4	21.9
Fast current	Pre Wisconsinan	31.8	29.2
Piscivorous	Pre Wisconsinan	31.4	26.5
Swim factor (0.25-0.35)	Pre Wisconsinan	28.3	26.5
Silt substratum	Pre Wisconsinan	27.7	24.6

Table 7. Loadings from principal component analysis of habitat and water quality data.

Attribute	PC 1	PC 2
Channel structure	-0.37	-0.13
Riffle %	-0.37	-0.03
Riffle run	-0.33	-0.08
Substrate type	-0.31	-0.09
Pool %	-0.30	-0.08
Pool glide	-0.27	-0.15
Riparian zone	-0.27	-0.10
Run %	-0.26	-0.03
Stream cover	-0.25	-0.16
Canopy cover %	-0.21	-0.05
Gradient	-0.11	0.35
Specific conductivity	-0.06	0.08
Dissolved oxygen (DO)	-0.01	-0.05
Water temperature	0.00	0.01
pH	0.01	-0.06
Turbidity	0.04	-0.13
Glide %	0.06	0.00
Water depth (mean)	0.11	-0.45
Water depth (max)	0.11	-0.43
Stream width (mean)	0.13	-0.44
Drainage area	0.14	-0.42

Table 8. Loadings from principal component analysis of hydrology variables.

IHA Parameter Group	PC 1
Rate and frequency of water condition changes	-0.51
Frequency and duration of high and low pulses	-0.51
Magnitude and duration of annual extreme water conditions	-0.50
Magnitude of monthly water conditions	-0.45
Timing of annual extreme water conditions	-0.18

Figure 1. Ohio River basin Wisconsin, Pre-Wisconsin, and unglaciated boundaries for Ohio, Indiana and Illinois.

Figure 2. Principal components analysis of taxonomic assemblages. Ellipses denote 95% confidence intervals. Separation of mean PCA axis scores for regions denotes significant differences as shown by a Tukey's multiple comparison test.

Figure 3. Principal components analysis of functional group assemblages. Ellipses denote 95% confidence intervals. Separation of mean PCA axis scores for regions denotes significant difference as shown by a Tukey's multiple comparison test.

Figure 4. Principal components analysis of habitat and water quality. Ellipses denote 95% confidence intervals. Separation of mean PCA axis scores for regions denotes significant differences as shown by a Tukey's multiple comparison test.

Appendix 1. Abundances of species included in analyses, by study region. Occurrence refers to percent of sites occupied within a study region.

Scientific Name	Common Name	Wisconsinan Abundance	Pre Wisconsinan Abundance	Unglaciaded Abundance	Wisconsinan Occurrence	Pre Wisconsinan Occurrence	Unglaciaded Occurrence
<i>Lampetra appendix</i>	American brook lamprey	271	4	294	0.009	0.004	0.009
<i>Etheostoma zonale</i>	banded darter	17512	6495	8363	0.225	0.301	0.222
<i>Cottus carolinae</i>	banded sculpin	0	27	382	0.000	0.001	0.018
<i>Hybopsis amblops</i>	bigeye chub	2349	1706	485	0.041	0.070	0.035
<i>Notropis boops</i>	bigeye shiner	47	657	93	0.005	0.044	0.007
<i>Hypophthalmichthys nobilis</i>	bighead carp	0	6	6	0.000	0.003	0.002
<i>Ictiobus cyprinellus</i>	bigmouth buffalo	79	62	32	0.013	0.040	0.010
<i>Ictiobus niger</i>	black buffalo	377	111	159	0.020	0.054	0.024
<i>Ameiurus melas</i>	black bullhead	1136	42	166	0.066	0.030	0.044
<i>Pomoxis nigromaculatus</i>	black crappie	1239	369	169	0.085	0.101	0.052
<i>Moxostoma duquesnei</i>	black redhorse	10024	4273	3983	0.153	0.258	0.144
<i>Percina maculata</i>	blackside darter	1306	279	1610	0.095	0.105	0.246
<i>Fundulus olivaceus</i>	blackspotted topminnow	0	0	161	0.000	0.000	0.015
<i>Fundulus notatus</i>	blackstriped topminnow	9572	462	776	0.189	0.098	0.063
<i>Cycleptus elongatus</i>	blue sucker	34	42	36	0.001	0.015	0.010
<i>Etheostoma camurum</i>	bluebreast darter	658	767	166	0.021	0.033	0.015
<i>Lepomis macrochirus</i>	bluegill	39621	9582	12634	0.635	0.735	0.625
<i>Etheostoma chlorosomum</i>	bluntnose darter	5	64	8	0.001	0.025	0.001

Scientific Name	Common Name	Wisconsinan Abundance	Pre Wisconsinan Abundance	Unglaciaded Abundance	Wisconsinan Occurrence	Pre Wisconsinan Occurrence	Unglaciaded Occurrence
<i>Pimephales notatus</i>	bluntnose minnow	229484	56813	97803	0.844	0.847	0.784
<i>Amia calva</i>	bowfin	57	11	54	0.007	0.011	0.022
<i>Noturus miurus</i>	brindled madtom	683	461	282	0.046	0.087	0.049
<i>Labidesthes sicculus</i>	brook silverside	847	420	670	0.059	0.113	0.082
<i>Culaea inconstans</i>	brook stickleback	987	12	3	0.031	0.006	0.001
<i>Ameiurus nebulosus</i>	brown bullhead	590	27	149	0.031	0.022	0.022
<i>Salmo trutta</i>	brown trout	704	122	10	0.014	0.017	0.004
<i>Pimephales vigilax</i>	bullhead minnow	2134	1915	1208	0.034	0.142	0.049
<i>Notropis percobromus</i>	carmine shiner	360	1	0	0.006	0.001	0.000
<i>Umbra limi</i>	central mudminnow	1526	6	22	0.059	0.003	0.007
<i>Campostoma anomalum</i>	central stoneroller	363791	121778	124251	0.730	0.726	0.699
<i>Ictalurus punctatus</i>	channel catfish	3358	1398	2140	0.148	0.302	0.175
<i>Notropis wickliffi</i>	channel shiner	30	12	349	0.002	0.007	0.018
<i>Ichthyomyzon castaneus</i>	chestnut lamprey	9	14	4	0.002	0.012	0.002
<i>Cyprinus carpio</i>	carp	17844	2241	2356	0.403	0.364	0.219
<i>Luxilus cornutus</i>	common shiner	17014	243	5609	0.061	0.018	0.083
<i>Semotilus atromaculatus</i>	creek chub	250234	37429	135613	0.806	0.617	0.781
<i>Erimyzon oblongus</i>	creek chubsucker	1821	38	301	0.064	0.019	0.032
<i>Etheostoma proeliare</i>	cypress darter	0	0	8	0.000	0.000	0.001
<i>Percina sciera</i>	dusky darter	680	383	606	0.034	0.088	0.079
<i>Ammocrypta pelluci</i>	sand darter	42	71	86	0.004	0.033	0.021

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<i>Notropis atherinoides</i>	emerald shiner	6615	8688	22114	0.056	0.239	0.144
<i>Etheostoma flabellare</i>	fantail darter	22075	10696	23963	0.362	0.542	0.574
<i>Pimephales promelas</i>	fathead minnow	15430	360	638	0.197	0.087	0.043
<i>Pylodictis olivaris</i>	flathead catfish	302	346	388	0.045	0.177	0.090
<i>Noturus nocturnus</i>	freckled madtom	8	4	3	0.001	0.006	0.001
<i>Aplodinotus grunniens</i>	freshwater drum	1757	1950	2200	0.062	0.219	0.152
<i>Notropis buechanani</i>	ghost shiner	0	0	96	0.000	0.000	0.003
<i>Dorosoma cepedianum</i>	gizzard shad	0	82	92	0.000	0.010	0.013
<i>Moxostoma erythrurum</i>	golden redhorse	28304	8427	13985	0.205	0.314	0.221
<i>Notemigonus crysoleucas</i>	golden shiner	27097	9898	13053	0.324	0.473	0.394
<i>Hiodon alosoides</i>	goldeye	2556	141	225	0.096	0.041	0.047
<i>Carassius auratus</i>	goldfish	738	12	7	0.038	0.014	0.004
<i>Ctenopharyngodon idella</i>	grass carp	7	4	9	0.002	0.006	0.006
<i>Esox americanus</i>	grass pickerel	3454	98	1032	0.147	0.043	0.152
<i>Erimystax x-punctatus</i>	gravel chub	1385	357	1076	0.027	0.058	0.046
<i>Lepomis cyanellus</i>	green sunfish	57846	9370	14882	0.785	0.701	0.699
<i>Etheostoma blennioides</i>	greenside darter	55847	20109	13921	0.536	0.502	0.390
<i>Etheostoma histrio</i>	harlequin darter	2	24	5	0.001	0.011	0.002
<i>Carpionodes velifer</i>	highfin carpsucker	186	195	116	0.015	0.083	0.035
<i>Nocomis biguttatus</i>	hornyhead chub	2615	53	237	0.063	0.010	0.014

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<i>Etheostoma nigrum</i>	johnny darter lake	36825	6500	18465	0.598	0.538	0.641
<i>Erimyzon sucetta</i>	chubsucker	7	0	0	0.001	0.000	0.000
<i>Micropterus salmoides</i>	largemouth bass	10445	1469	2637	0.458	0.415	0.395
<i>Campostoma oligolepsis</i>	largescale stoneroller	2374	1188	571	0.019	0.025	0.010
<i>Lampetra aepyptera</i>	least brook lamprey	100	256	1485	0.009	0.065	0.148
<i>Etheostoma microperca</i>	least darter	782	2	0	0.023	0.003	0.000
<i>Percina caprodes</i>	logperch	8380	3325	2981	0.262	0.400	0.275
<i>Lepomis megalotis</i>	longear sunfish	35056	22233	17052	0.368	0.648	0.398
<i>Rhinichthys cataractae</i>	longnose dace	0	0	142	0.000	0.000	0.003
<i>Lepisosteus osseus</i>	longnose gar	207	191	392	0.035	0.109	0.077
<i>Notropis volucellus</i>	mimic shiner	1859	2067	2852	0.043	0.135	0.100
<i>Hybognathus nuchalis</i>	Mississippi silvery minnow	304	768	75	0.006	0.065	0.008
<i>Ichthyomyzon greeleyi</i>	mountain brook lamprey	75	0	0	0.003	0.000	0.000
<i>Hiodon tergisus</i>	mooneye	12	24	36	0.003	0.022	0.010
<i>Cottus bairdi</i>	mottled sculpin	56710	8719	20395	0.280	0.185	0.175
<i>Noturus eleutherus</i>	mountain madtom	42	124	9	0.003	0.029	0.004
<i>Etheostoma asprigene</i>	mud darter	2	117	58	0.001	0.040	0.009
<i>Esox masquinongy</i>	muskellunge	23	1	17	0.004	0.001	0.008
<i>Ichthyomyzon fossor</i>	northern brook lamprey	16	0	0	0.002	0.000	0.000
<i>Hypentelium nigricans</i>	hogsucker	48498	17390	21106	0.487	0.572	0.535

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<i>Noturus stigmosus</i>	madtom	0	34	2	0.000	0.012	0.001
<i>Esox lucius</i>	northern pike	132	0	79	0.013	0.000	0.024
<i>Fundulus catenatus</i>	northern studfish	22	0	0	0.003	0.000	0.000
<i>Lepomis humilis</i>	orangespotted sunfish	1883	241	394	0.080	0.076	0.029
<i>Etheostoma spectabile</i>	orangethroat darter	17436	2523	3236	0.295	0.228	0.122
<i>Aphredodeus sayanus</i>	pirate perch	111	146	200	0.004	0.040	0.035
<i>Notropis ariommus</i>	popeye shiner	0	2	24	0.000	0.001	0.004
<i>Opsopoeodus emiliae</i>	pugnose minnow	1	69	29	0.000	0.014	0.004
<i>Lepomis gibbosus</i>	pumpkinseed	3004	30	268	0.111	0.018	0.046
<i>Carpiodes cyprinus</i>	quillback	2143	810	765	0.124	0.207	0.102
<i>Etheostoma caeruleum</i>	rainbow darter	73617	19589	12941	0.502	0.531	0.356
<i>Oncorhynchus mykiss</i>	rainbow trout	35	0	6	0.005	0.000	0.003
<i>Cyprinella lutrensis</i>	red shiner	350	0	5	0.003	0.000	0.001
<i>Lepomis microlophus</i>	redeer sunfish	313	112	180	0.022	0.034	0.054
<i>Lythrurus umbratilis</i>	redfin shiner	4035	708	2852	0.072	0.090	0.127
<i>Clinostomus elongatus</i>	redside dace	3633	738	2394	0.040	0.043	0.074
<i>Lythrurus fumeus</i>	ribbon shiner	2	187	206	0.000	0.030	0.007
<i>Carpiodes carpio</i>	river carpsucker	2206	1127	303	0.051	0.172	0.043
<i>Nocomis micropogon</i>	river chub	4758	640	2025	0.060	0.051	0.066
<i>Percina shumardi</i>	river darter	8	1	8	0.000	0.001	0.004
<i>Moxostoma carinatum</i>	river redhorse	418	88	242	0.031	0.043	0.034
<i>Notropis blennius</i>	river shiner	1651	168	1	0.003	0.019	0.001
<i>Ambloplites rupestris</i>	rock bass	19956	4581	5044	0.434	0.461	0.398

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<i>Notropis rubellus</i>	rosyface shiner	12334	4965	5475	0.122	0.145	0.119
<i>Clinostomus funduloides</i>	rosyside dace	0	0	601	0.000	0.000	0.014
<i>Notropis ludibundus</i>	sand shiner	63233	18675	14920	0.382	0.444	0.270
<i>Stizostedion canadense</i>	sauger	315	227	232	0.033	0.102	0.054
<i>Lythrurus ardens</i>	scarletfin shiner	8492	3932	2434	0.150	0.230	0.095
<i>Macrhybopsis hyostoma</i>	shoal chub	9	44	0	0.001	0.010	0.000
<i>Moxostoma macrolepidotum</i>	shorthead redhorse	3807	1496	892	0.079	0.142	0.072
<i>Lepisosteus platostomus</i>	shortnose gar	18	52	74	0.002	0.029	0.006
<i>Scaphirhynchus platyrhynchus</i>	shovelnose sturgeon	4	5	1	0.001	0.004	0.001
<i>Macrhybopsis storeriana</i>	silver chub	12	58	36	0.002	0.028	0.011
<i>Hypophthalmichthys molitrix</i>	silver carp	0	8	2	0.000	0.008	0.001
<i>Ichthyomyzon unicuspis</i>	silver lamprey	22	11	16	0.005	0.008	0.010
<i>Moxostoma anisurum</i>	silver redhorse	2244	793	1668	0.108	0.174	0.159
<i>Notropis photogenis</i>	silver shiner	10081	2744	3639	0.193	0.183	0.139
<i>Notropis shumardi</i>	silverband shiner	2	86	0	0.000	0.004	0.000
<i>Ericymba buccata</i>	silverjaw minnow	31013	11284	17694	0.353	0.455	0.459
<i>Alosa chrysochloris</i>	skipjack herring	102	87	371	0.007	0.040	0.027
<i>Percina phoxocephala</i>	slenderhead darter	244	337	257	0.027	0.114	0.032
<i>Etheostoma gracile</i>	slough darter	1	139	36	0.000	0.044	0.013
<i>Micropterus dolomieu</i>	Smallmouth b	19658	6084	5002	0.361	0.465	0.306

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<i>Ictiobus bubalus</i>	smallmouth buffalo	1060	809	1020	0.032	0.138	0.057
<i>Moxostoma breviceps</i>	smallmouth redhorse	375	1160	2008	0.011	0.054	0.060
<i>Phoxinus erythrogaster</i>	southern redbelly dace	16837	2682	16810	0.118	0.092	0.258
<i>Cyprinella spiloptera</i>	spotfin shiner	39378	18572	19004	0.386	0.563	0.356
<i>Etheostoma squamiceps</i>	spottail darter	0	12	26	0.000	0.003	0.005
<i>Micropterus punctulatus</i>	spotted bass	3398	1978	3483	0.143	0.392	0.256
<i>Etheostoma maculatum</i>	spotted darter	16	5	70	0.003	0.004	0.003
<i>Lepisosteus oculatus</i>	spotted gar	0	0	9	0.000	0.000	0.004
<i>Minytrema melanonps</i>	spotted sucker	1699	114	375	0.098	0.052	0.086
<i>Cyprinella whipplei</i>	steelcolor shiner	3242	1963	590	0.054	0.179	0.046
<i>Noturus flavus</i>	stonecat	1902	704	506	0.123	0.210	0.096
<i>Erimystax dissimilis</i>	streamline chub	434	158	407	0.020	0.028	0.018
<i>Morone saxatilis</i>	striped bass	6	10	2	0.001	0.010	0.001
<i>Luxilus chrysocephalus</i>	striped shiner	92609	24156	53016	0.538	0.535	0.582
<i>Etheostoma kennicotti</i>	stripetail darter	0	0	75	0.000	0.000	0.005
<i>Phenacobius mirabilis</i>	suckermouth minnow	8757	1115	710	0.126	0.128	0.051
<i>Noturus gyrinus</i>	tadpole madtom	502	33	24	0.034	0.018	0.011
<i>Dorosoma petenense</i>	threadfin shad	56	36	16	0.001	0.007	0.001
<i>Etheostoma tippecanoe</i>	Tippecanoe darter	282	60	71	0.013	0.014	0.005
<i>Exoglossum laurae</i>	tonguetied minnow	257	0	0	0.008	0.000	0.000

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<i>Percopsis omiscomaycus</i>	troutperch	1419	59	932	0.032	0.011	0.089
<i>Etheostoma variatum</i>	variegate darter	949	381	1216	0.026	0.058	0.049
<i>Stizostedion vitreum</i>	walleye	100	9	15	0.012	0.007	0.010
<i>Lepomis gulosus</i>	warmouth	489	106	322	0.037	0.047	0.086
<i>Rhinichthys atratulus</i>	western blacknose dace	123258	14896	33100	0.448	0.286	0.446
<i>Gambusia affinis</i>	western mosquitofish	79	914	269	0.005	0.092	0.029
<i>Morone chrysops</i>	white bass	155	172	408	0.027	0.094	0.047
<i>Pomoxis annularis</i>	white crappie	2037	599	2210	0.111	0.135	0.094
<i>Catostomus commersoni</i>	white sucker	110845	17751	32009	0.737	0.550	0.638
<i>Morone mississippiensis</i>	yellow bass	10	9	0	0.001	0.003	0.000
<i>Ameiurus natalis</i>	yellow bullhead	9582	2223	3435	0.451	0.433	0.415
<i>Perca flavescens</i>	yellow perch	1511	65	128	0.046	0.021	0.024