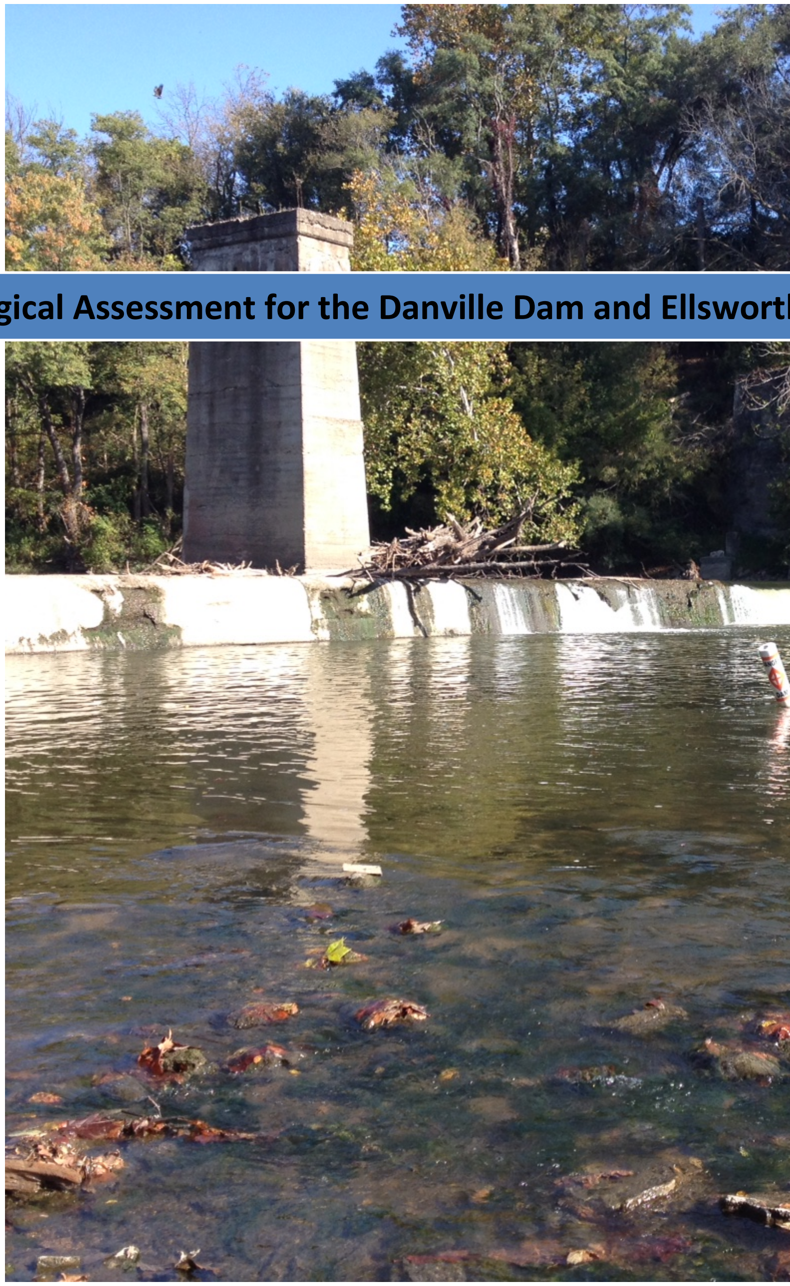

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Biological Assessment for the Danville Dam and Ellsworth Park Dam Removal Projects

FY 2012 State Wildlife Grant

Final Report

March 2018

Submitted by:

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Division of Fisheries

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Final Report (March 2018)

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GRANT TITLE: Biological Assessment for the Danville Dam and Ellsworth Park Dam Removal Projects

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INTRODUCTION: Impoundments are one of the major sources of anthropogenic disturbances on streams. Dam effects include converting lotic habitats to lentic habitats, changing flow regimes, altering physicochemical parameters, increasing siltation upstream and scouring substrates downstream from the dam, and altering fish assemblages and/or blocking movement of fishes. The resultant dam effects can alter aquatic assemblages (e.g., fishes, freshwater mussels, and aquatic insects), including reduced native species richness and abundance, as well as restricted distributions and isolated populations.

The 11-foot high Danville Dam, constructed in 1914, serves as the downstream-most impoundment between the Wabash River and the Vermilion River basin. The dam is an effective barrier between the lower 22 miles of the Vermilion River mainstem and the 1,290 mi^2 drainage area upstream, hindering distribution of several aquatic organisms, including 96 species of fish and 46 species of mussels. The dam is also a safety hazard with three drownings in the past ten years.

Ellsworth Park Dam is a low-head dam constructed in 1920, near the confluence of the North Fork Vermilion River with the Vermilion River. This outdated dam serves as a barrier to approximately four river miles of excellent habitat downstream of Lake Vermilion. This dam is the site of one drowning in recent years.

Danville Dam on the Vermilion River and Ellsworth Park Dam on the North Fork Vermilion River are slated for removal in 2018. This dam removal project will remove a barrier to 1,115 stream miles upstream of these dams in the Vermilion River basin, benefitting an extraordinarily high number of Species in Greatest Need of Conservation (83) of the Illinois Wildlife Action Plan (33 mollusks, 28 fish, 15 amphibians, 5 reptiles, and 2 crustaceans,). Dam removal also has been identified as a priority in the Vermilion River Conservation Opportunity Area Plan (Goal 2, Objective 4, Strategy 1). The project also addresses four of the Ohio River Basin Fish Habitat Partnership Strategic Actions: protecting healthy waters, restoring natural variability in river and stream flows, reconnecting fragmented stream habitat, and reducing altered temperature and oxygen levels.

Benefitting species include two federally listed mussel species (Northern Riffleshell and Clubshell), 26 state-listed species, and many game species, including Smallmouth Bass. The project will also open downstream access to the Middle Fork Vermilion River, Illinois' only National Scenic River.

The benefits of removing these barriers within the Vermilion River basin are potentially monumental in scope. Progress toward these goals warrants monitoring and documentation in order to affirm success and advise adaptive management and additional needs.

PURPOSE: State Wildlife Grant funding was utilized to assess baseline biotic and abiotic conditions in the Vermilion River and North Fork Vermilion River to determine current conditions upstream and downstream of Danville Dam on the Vermilion River and Ellsworth Park Dam on the North Fork Vermilion River. Results from these monitoring efforts will help guide plans for the dam removal and potential channel modifications, and will allow us to monitor and evaluate changes in the biological communities and various abiotic metrics following dam removal. Few dam removal studies that fully address biologic responses among multiple organism groups (fish, mussels, and macroinvertebrates) have been published. This study will contribute significantly to the growing body of literature.

OBJECTIVES:

1. Conduct fish population surveys at 12 stations, twice per year in spring and fall of 2014 and 2015 and once in spring of 2016 (5 replicates).

2. Conduct mussel surveys at 12 stations, once in summer of 2014 and once in summer of 2016 (2 replicates).

3. Conduct macroinvertebrate surveys at 12 stations, twice per year in spring and fall of 2014 and 2015 and once in spring of 2016 (5 replicates).

4. Conduct habitat quality assessments at 12 stations, twice per year in spring and fall of 2014 and 2015 and once in spring of 2016 (5 replicates).

5. Collect seasonal water quality samples at 6 stations, at least four times per year in 2014 and 2015 and once in 2016, at three sites per dam, testing for suspended solids, hardness, alkalinity, chlorophyll, phosphates and nitrates.

6. Collect tissue samples from up to 25 Black Redhorse from 12 stations for genetic analyses.

EXPECTED BENEFITS AND RESULTS: This dam removal project will remove a barrier to 1,115 stream miles (190 mi^2 of watershed) upstream of Danville Dam in the Vermilion River basin, benefitting an extraordinarily high number of Species in Greatest Need of Conservation (83) of the Illinois Wildlife Action Plan (33 mollusks, 2 crustaceans, 28 fish, 15 amphibians, 5 reptiles). With the Vermilion River basin being one of the most biologically significant basins in the state, identified as a Conservation Opportunity Area for the state of Illinois, biological monitoring of this critical act of dam removal is imperative.

Intensive collection of biotic and abiotic baseline conditions will allow us to determine current influences of these dams. We will further use these data to guide the decision-making process for the dam removals and potential channel modifications and habitat improvements following dam removal. Collection of these data will also allow us to compare and track changes that develop, following the dam removals. This will allow us to gauge the results of the project and advise any necessary adaptive management actions. Finally, comprehensive data from this project will be used to manage future proposed dam removal projects.

APPROACH: To assess the impacts of removing the Ellsworth Park and Danville dams on the aquatic biota and stream habitat quality, a three phase project on this system was initiated. Beginning October 2012, assessment of the fish and macroinvertebrate assemblages in twelve, 100 meter long sections of river began. Six of the 12 sites surveyed were located in the North Fork Vermilion River, referred to as Ellsworth Dam sites and six sites in the Vermilion River, referred to as Danville Dam sites. Each dam assessment consists of two sites below the dam and four sites above the dam. The above dam sites consist of locations directly above the dam, the last 100 meters of the pool, the first 100 meters of the river and an upstream site (a further upstream location). This sampling captures the community composition both above and below the dam (immediate impacts) and characteristics of sites above the dam's influence.

COMPLIANCE: The IDNR used its CERP (Comprehensive Environmental Review Process) as a tool to aid the Department in meeting NEPA compliance for the projects outlined under this grant proposal. It is the Department's policy to require CERP applications for all land disturbing activities unless those activities are covered by CERP exemptions.

All activities were in compliance with the Endangered Species Act. All determinations and documentation are in accordance with the current established U.S. Fish and Wildlife Service protocols for Section 7.

All activities were in compliance with the National Historic Preservation Act and the Council on Historic Preservation Act. All determinations and documentation were in accordance with the terms of the Programmatic Agreement, as amended.

Planned activities which involve a floodplain and/or jurisdiction of wetlands will be done in accordance with Presidential Executive Orders 11988 and 11990.

GEOGRAPHIC LOCATION: The Vermilion River basin (Wabash River drainage) is located in east central Illinois (parts of Livingston, Ford, Iroquois, Champaign, and Vermilion counties) and western Indiana (parts of Warren and Vermillion counties). It drains 1,434 mi^2, and its basin includes the Salt Fork sub-basin (506 mi^2), the Middle Fork sub-basin (438 mi^2) and the North Fork sub-basin (294 mi^2). It flows through two natural divisions: Wabash Border and Grand Prairie.

The Danville Dam [Latitude: 40.12225N & Longitude: 87.63156W] is located about 22 miles upstream from the confluence with the Wabash River, and is located downstream of the Highway 150/1 bridge in

Danville, Vermilion County, Illinois. The dam is located in Congressional District 15. The 8-digit HUC number is 05120109.

The Ellsworth Park Dam is less than one mile upstream on the North Fork Vermilion River, southwest of the aforementioned highway intersection [Latitude: 40.12547N & Longitude: 87.63922W].

Figure 1 – Location of the Danville Dam and Ellsworth Park Dam. The dams are located in Danville, Vermilion County, Illinois.

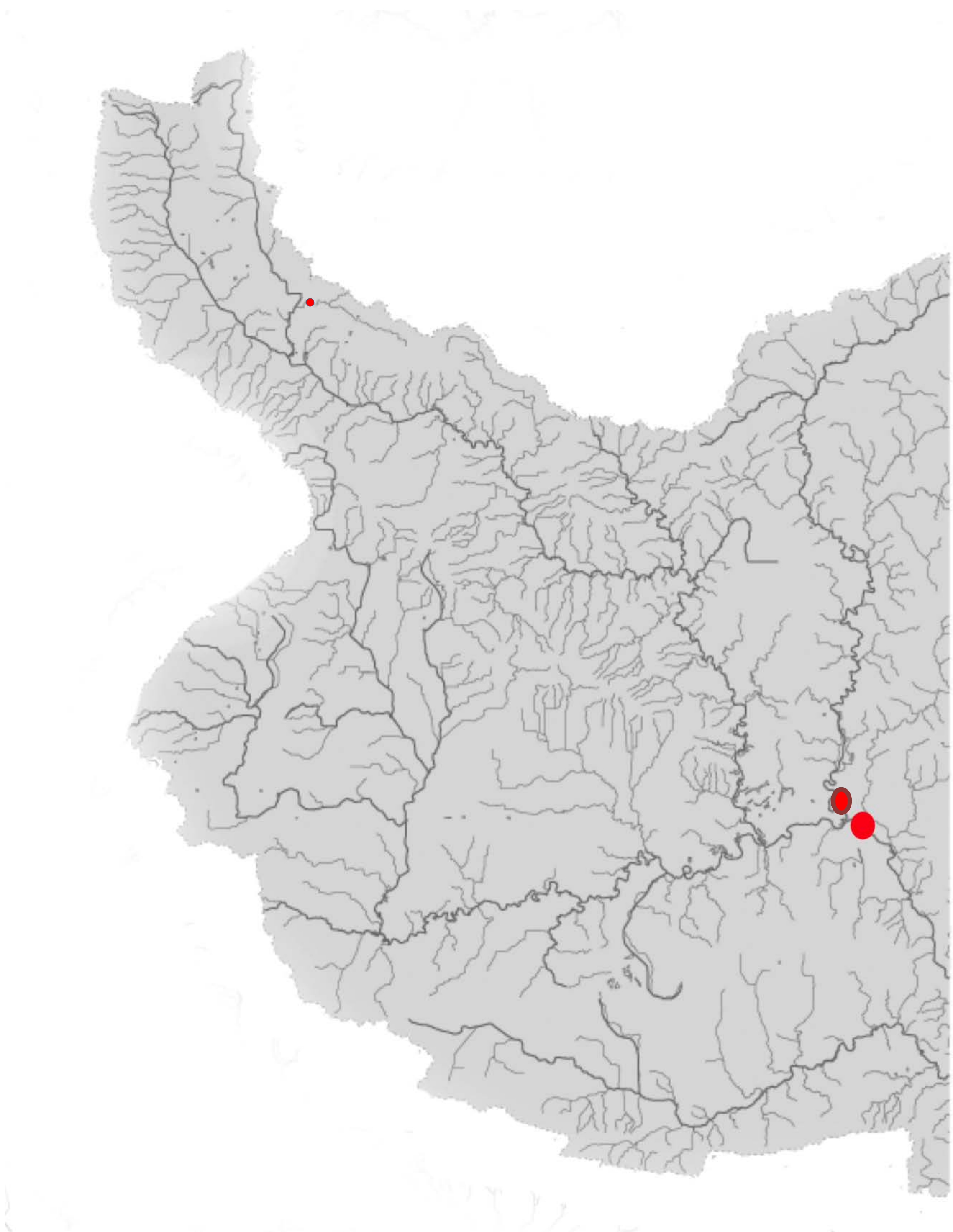

Figure 2 – Location of the Danville Dam and Ellsworth Park Dam within the Vermilion River basin (Wabash River drainage).

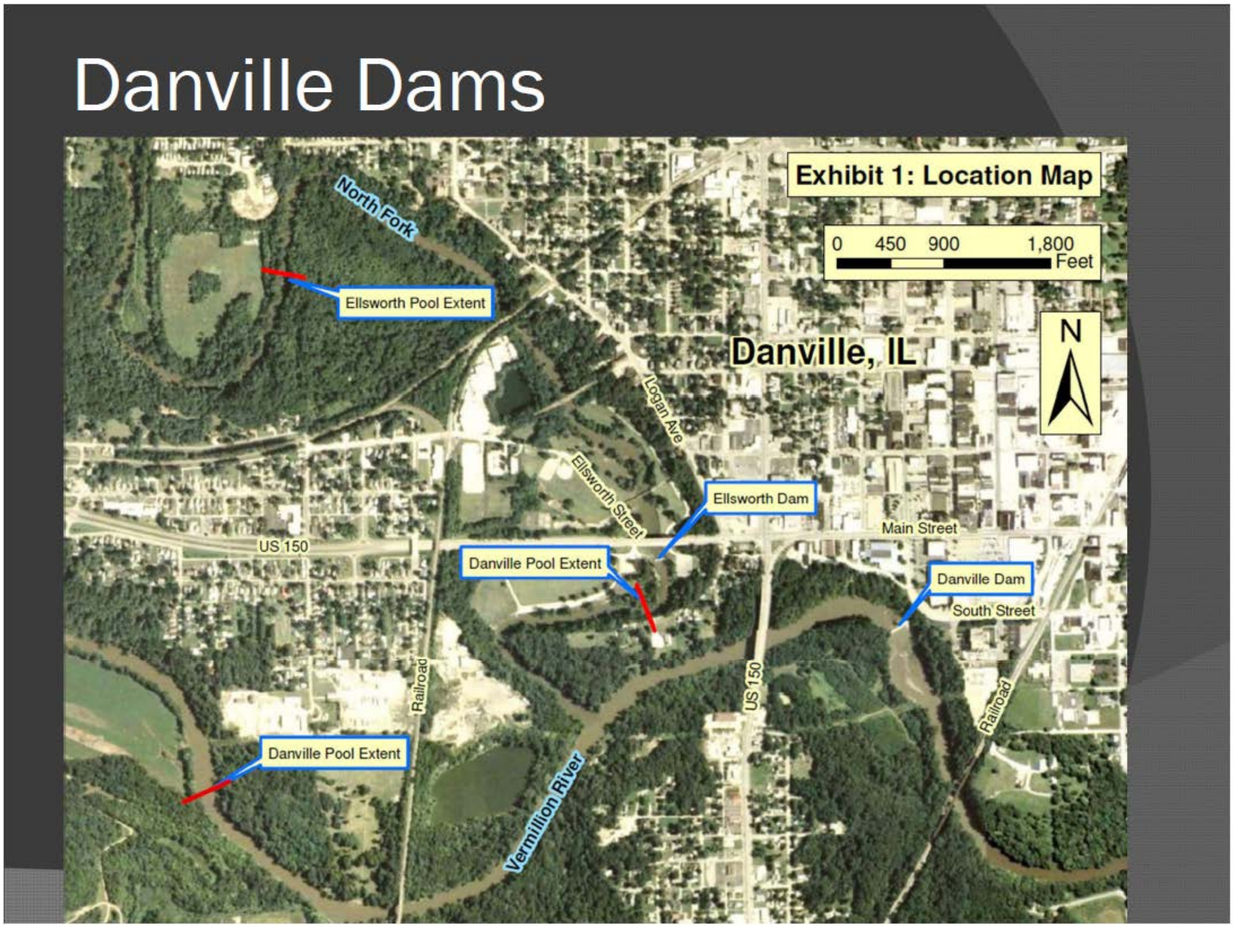

Figure 3 – Plan overview of the Danville Dam and Ellsworth Park Dam, illustrating the approximate pool impacts of each dam.

Figure 4 – Map showing the locations of the 12 sampling stations.

Figure 5 – Danville Dam on the Vermilion River. Photo taken on January 2, 2014 showing continued structure failure.

Figure 6 – Danville Dam during above normal flow conditions, fish ladder in foreground.

Figure 7 – Danville Dam photo from October 14, 2015 showing seepage along the face of the dam during low flow conditions.

Figure 8 – Ellsworth Park Dam on the North Fork Vermilion River. Photo was taken on June 18, 2015 during above normal flow conditions.

METHODOLOGY

Job 1. Conduct fish population surveys at 12 stations (5 replicates).

Eastern Illinois University researchers utilized a multiple gear approach for fish sampling, needed to maintain consistency before and after dam removals. Ellsworth Park Dam fish shocking used DC barge shocking with a 2,500 watt generator with a five person crew, three probe/netters and two extra netters. Each site was electrofished for a total of 30 minutes beginning downstream and moving upstream. Danville Dam sites were sampled using DC boat shocking with a 4,000 watt generator with two spider array droppers and a single netter for a total of 30 minutes across the entire area. This reflects the larger nature of this channel. Two seine hauls were conducted for all Danville Dam sites at the nearest sandbar. The seine samples were needed to ensure collection of smaller fish the DC boat shocking was not likely to capture. All fish over 100 mm were measured to the nearest millimeter in total length and weighed to the nearest gram. Cyprinids and fish fewer than 100 mm were euthanized and preserved in 10% formalin solution for identification in the laboratory.

Surveys of the 12 sites described above were conducted in the spring and fall by Eastern Illinois University researchers, with target dates in May and September depending on flow conditions. The sites were sampled twice per year in 2014 and 2015, and culminated with a spring sample in 2016.

Species richness and diversity were calculated for fish for each site using methods from Lande 1996. An index of biotic integrity for fish at each site was calculated using methods from Angermeier and Karr 1986. A multiple analysis of variance (MANOVA) was conducted to test the significance of abiotic factors (see Job 4) and community structure. An ANOVA was used to test for significance of habitat quality (see Job 4) of individual sites pre- and post-removal of the dams.

Job 2. Conduct mussel surveys at 12 stations (2 replicates).

Live freshwater mussels and valves of dead specimens were collected by hand grubbing for four person-hours at each of the 12 sites described above by an Illinois Natural History Survey (INHS) mussel crew. Mussels were identified, measured (shell length), aged, and if possible, live individuals were sexed before returning them to the site. Voucher specimens (dead shell) of all species were taken at each site to be deposited in the INHS Mollusk Collection. An effort to sample all available habitats was made, but particular emphasis was placed on areas that appeared likely to support freshwater mussels (e.g., gravel riffles, runs, and pools). The INHS Mollusk Collection was consulted to determine historical records (eg., presence/absence). Regarding nomenclature, the list of common and scientific names of mollusks prepared by the Council of Systematic Malacologists and the Committee on Scientific and Common Names of the American Malacological Union was followed, except subspecies were not recognized. Freshwater mussel abundance and richness (number of species) were calculated. Analysis of variance (ANOVA) was conducted to test the significance of community structure.

Mussel surveys were conducted pre-dam removal during the summer of 2014 (July to August). Post-dam removal surveys were not conducted, due to delays in the dam removal schedule. This information is being used to assess the baseline condition of the freshwater mussel population pre-dam removal and will be used to assess immediate response of the mussel populations post-dam removal. These collection data will be further used to compare to periodic post-dam removal collections for years to come, as mussel populations are likely to take several years to colonize the previously impounded reaches.

Job 3. Conduct macroinvertebrate surveys at 12 stations (5 replicates).

Macroinvertebrate surveys were conducted at the 12 stations described above by Eastern Illinois University researchers. The macroinvertebrate sampling for the four upper Danville Dam sites, which are non-wadeable, include a random set of 20 jabs. In order to ensure consistency, seven random jabs (D-frame net, based on habitat percentages from QHEI assessments) were conducted on each bank side and six ponar grabs in the main channel.

Macroinvertebrate communities were assessed at all wadeable sites using a multi-habitat set of 20 jabs, based on habitat percentages from QHEI assessments. All macroinvertebrate samples were preserved in 95% ethanol for identification in the laboratory. A subset of 300 macroinvertebrates was sampled using sample splitter and identified to the lowest taxonomic group possible. Macroinvertebrate surveys were conducted at the same frequency and timeframe as the fish surveys.

Job 4. Conduct habitat quality assessments at 12 stations (5 replicates).

Habitat quality assessments were conducted by Eastern Illinois University researchers. Habitat for the non-wadeable upper Danville Dam sites were assessed through the stream habitat assessment protocol (non-wadeable sites, n =4). Habitat quality was assessed at all wadeable sites using the Ohio Qualitative Habitat Evaluation Index (wadeable sites, n =8). Habitat data will be used to identify physical changes following dam removal, and as abiotic factors in the analyses of the biotic data. Habitat surveys were conducted at the same frequency and timeframe as the fish surveys.

Job 5. Collect seasonal water quality samples at 6 stations, testing for suspended solids, hardness, alkalinity, chlorophyll, phosphates and nitrates.

Water samples were collected seasonally by Eastern Illinois University researchers, at least four times per year, at three sites per dam. Water was collected below the dam, in the pool above the dam, and in the first 100 meters of the river above the pool. A YSI multi meter was used to determine PH, temperature, conductivity and dissolved oxygen on site. Samples brought back to Eastern Illinois University were analyzed for suspended solids, hardness, alkalinity, chlorophyll, phosphates and nitrates using standard methods. Samples will be used to identify changes in water quality following dam removal, and as abiotic factors in the biotic analyses.

Job 6. Conduct genetic analyses of Black Redhorse

All tissue samples were collected during monitoring activities, as described under Job 1 above. Genetic analyses: 1. Determine the impact dam construction has had on the genetic diversity and differentiation of Black Redhorse populations in the Vermillion River. 2. Determine how Black Redhorse initially respond to dam removal and alteration. 3. Create baseline data for future analyses investigating the long-term genetic effects dam construction has on fish populations after dam removal.

Genetic sampling required removal of an approximately 5mm^2 portion of dorsal fin tissue before live fish were released and after identification of preserved fish. Tissue samples were stored in 95% ethanol for DNA extraction. Up to 25 fish were sampled for genetic analyses at each site.

Genetic work was done in the lab of Dr. Devon Keeney at Le Moyne College in Syracuse, New York. DNA was isolated from up to 25 Black Redhorse from each site using a standard chelex-proteinase K extraction protocol. A set of 10-12 microsatellite markers was used to analyze the genetic variation and differentiation within and among populations. Microsatellites consist of tandem repeats of DNA, such as CACACACA, and are highly variable within populations, facilitating the accumulation of genetic differences among isolated populations. A combination of preexisting and novel microsatellites developed in Dr. Keeney's lab was utilized. Microsatellite amplifications used fluorescent-labeled DNA primers in multiplex polymerase chain reactions (PCRs). Raw multiplex genotype data was generated using the 3730xl 96-Capillary Genetic Analyzer at Yale University's Core DNA Analysis Facility and analyzed at Le Moyne College.

RESULTS

The studies conducted under this State Wildlife Grant culminated in a series of published, and yet to be published, reports. Those reports are included here to present the results of the funded studies.

Job 1-5. Results from Jobs 1-5 are presented in four publications listed below and included in the following pages.

"Contrasting Impacts of Dams on the Metacommunity Structure of Fish and Macroinvertebrate Assemblages" by Hastings et al. was published in the *North American Journal of Fisheries Management* in 2016. Results from Job 1, 3, and 4 are presented.

"When to sample: flow variation mediates low-head dam effects on fish assemblages" by Hastings et al. was published in the *Journal of Freshwater Ecology* in 2016. Results from Job 1 are presented.

"Effects of Lowhead Dams on Freshwater Mussels in the Vermilion River Basin, Illinois, with Comments on a Natural Dam Removal" by Tiemann et al. was published in the *Transactions of the Illinois State Academy of Science* in 2016. Results from Job 2 are presented.

"Low-head Dam Impacts on Habitat and the Functional Composition of Fish Communities" by Smith et al. was accepted by River Research and Applications in 2016. Results from Job 1 and 4 are presented.

Job 6. Conduct genetic analyses of Black Redhorse

Job 6 was a late amendment to this grant, and initiation of the contracted work was delayed by the state budget impasse. As a result, the genetic analyses are incomplete and ongoing. The preliminary results completed to this point are included here.

The goals for this job are to: 1) develop and optimize 10-12 microsatellite loci for investigating the impact the Danville and Ellsworth Park Dams have had on the genetic diversity and genetic structure of black redhorse (*Moxostoma duquesnei*) populations within the Vermilion River system. During the quarter spanning October 1 – December 31 2017, twelve microsatellite loci previously optimized in our lab (Table 1) were utilized on 116 "black" redhorse DNAs. Preliminary analyses revealed the presence of two distinct genetic groups and several microsatellite loci consistently failed to amplify in one of these groups. These results suggested the presence of two distinct species. To test this, the COI DNA barcode region was sequenced and analyzed from ten redhorse from each genetic group. Sequencing revealed that the two groups were black redhorse (*Moxostoma duquesnei*) and golden redhorse (*Moxostoma erythrurum*). Due to the presence of golden redhorse identified as black redhorse, DNA was extracted from a larger number of redhorse to increase the sample size of the target species. DNA has been extracted from 382 redhorse: 260 fish identified as black redhorse in the field and 122 fish identified as golden redhorse in the field. Due to the need to extract DNA and genotype additional fish, genotyping continued through December and is now complete. Current analyses focus on identifying fish species. The COI Barcode region has been sequenced from 96 fish, and results are consistent with the presence of two species. DNA results to date suggest that approximately 50% of fish identified as black redhorse are golden redhorse (Fig. 1). We will therefore have comparative data on the impact of the dams on the genetic diversity and genetic structure of both species and investigate if there is evidence of hybridization between these species. Given the need to identify genetic species, analyses of genetic diversity and structure are just beginning with both species. This work is ongoing due to the need to include a larger sample of fish, including an additional species.

Table 1. Microsatellite loci optimized for black redhorse analyses.

Microsatellite Locus	DNA Motif
BLR 2022	$(ACTC)_9$
BLR 447	$(AAAC)_9$
BLR 1343	$(ACTC)_{12}$
BLR 1571	$(AGAT)_{14}$
BLR 69	$(AATC)_{12}$
BLR 609	$(ACAG)_{12}$
BLR 720	$(ACAT)_{11}$
BLR 761	$(ACTC)_{16}$
DLU 45	$(GATA)_{29}$
DLU 405	$(GATA)_{21}$
BLR 1027	$(ATCC)_{12}$
BLR 2268	$(ACAG)_{13}$

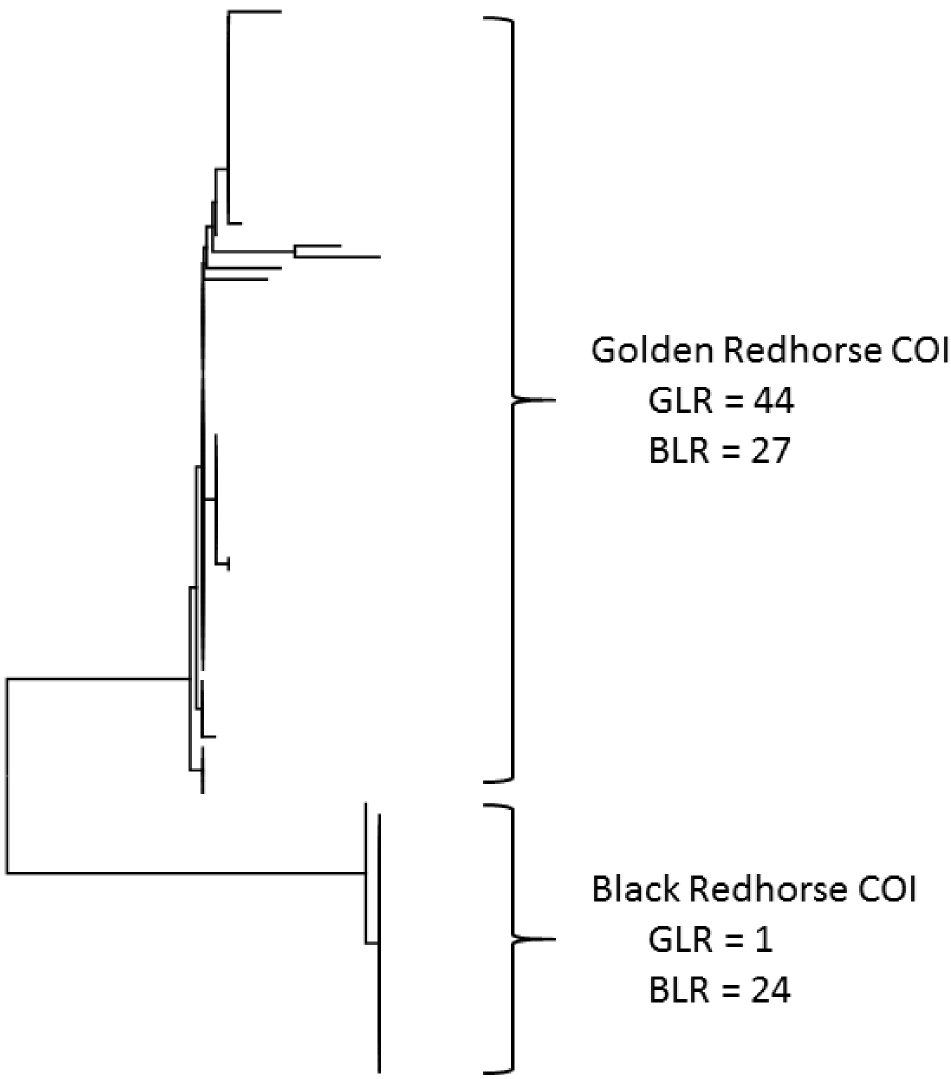

Fig. 1. Neighbor-joining phylogenetic tree of redhorse COI DNA sequences. Two major clades indicate golden and black redhorse COI DNA. Field species identifications of fish within each clade are indicated by "GLR" for golden redhorse and "BLR" for black redhorse.

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ARTICLE

Contrasting Impacts of Dams on the Metacommunity Structure of Fish and Macroinvertebrate Assemblages

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Abstract
Impoundments are common features of many rivers that often impact abiotic conditions and the organisms that inhabit impacted reaches. As dams alter both local environmental conditions and the ability of organisms to move throughout the habitat, it is difficult to know which factors are driving changes in assemblage composition. To separate these effects, we employed a metacommunity approach to evaluate drivers of assemblage composition in fish and macroinvertebrate communities across two impoundments slated for removal in Danville, Illinois. Based on movement ability, we would expect dams to represent barriers to fish populations, whereas macroinvertebrates, with their motile adult phases, should be easily able to move across impoundments. Therefore, we would expect the assemblage structure of these two groups to be driven by different processes. We sampled habitat quality (measures) and both fish and macroinvertebrate communities in a replicated series of sites across two low-head dams. As expected, the presence of dams resulted in reduced habitat quality as well as changes in fish and macroinvertebrate quality indices. However, fish and macroinvertebrate assemblages were driven by different metacommunity processes. Fish communities showed strong environmental filtering, responding to local environmental conditions, with no effect of distance between habitats. In marked contrast, macroinvertebrate communities were only related to physical distance between sites, with no indication of environmental filtering. These results suggest that when these dams are removed, fish assemblages should change with the removal of dam-generated habitats. In contrast, dam removal may not alter macroinvertebrate composition, as it did not vary with habitat but appears driven by local dispersal.

Dams are a major source of anthropogenic disturbance on river systems. Historically, dams were constructed to provide a wide array of services: power generation, flood control, navigation, water supply, and recreation (Bednarek 2001; Liermann et al. 2012). As many dams have outlived their economic usefulness and likely generate ecological impacts, they are increasingly being removed to reestablish natural conditions and to increase safety (Hart et al. 2002; Poff and Hart 2002). For this reason, understanding the impacts of dams and predicting the effects of dam removal are critical for the management of riverine systems.

Metacommunities are local biological communities in a landscape that are connected, at least partially, by dispersal (Leibold et al. 2004). As dams alter both abiotic conditions and habitat connectivity, metacommunity theory can be used as a conceptual framework to understand how communities assemble in these fragmented landscapes. More importantly, this framework can be used to isolate the individual influences of dams and therefore can be used to predict the effects of dam removal. Taxa may vary in their metacommunity responses to dams, generating heterogeneity in the drivers that control community composition across taxonomic groups. Leibold

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(2009) outlined four paradigms to model metacommunity dynamics, including mass effects, patch dynamics, neutral dynamics, and species sorting. Of these, patch dynamics, species sorting, and neutral dynamics appear particularly important for impounded river systems. Understanding how dams control metacommunity structure may directly suggest ways to ameliorate their impacts and predict the impacts of dam removal.

According to the patch dynamics paradigm, variation in community composition is generated by patterns of extinction and colonization of individual patches. Within river systems, dispersal and recolonization are important for community stability (Taylor et al. 2006; Slawski et al. 2008; Heino 2012), and dams primarily function as physical barriers to dispersal (Martinez et al. 1994; Nislow et al. 2011), altering colonization rates of biota at multiple life history stages. While dams are primarily barriers to dispersal, episodic release events also have the potential to cause surges that disperse many organisms downstream (Vehanen et al. 2005). The presence of barriers can cause shifts in fish community structure by not allowing organisms to move freely throughout the system (Guenther and Spacie 2006). Though some impoundments mitigate reduced dispersal via fish ladders, side channels, or pumps, they may still restrict dispersal (Nislow et al. 2011). Dams may also prevent species migration because of physical changes in the environment that act as a behavioral deterrent rather than as a physical barrier (Taylor et al. 2008). While stream macroinvertebrates are primarily aquatic, many taxa have flying adult stages (Wallace and Anderson 1996; Hershey and Lamberti 2001; Karna et al. 2015) which should not respond to low-head dams as barriers. However, macroinvertebrate eggs are released into waters and may drift appreciable distances based on flow (Bilton et al. 2001). Therefore, dams have the potential to alter dispersal rates in both fish and macroinvertebrates. Dam-induced restrictions on dispersal should generate communities that become increasingly dissimilar with increasing distance, but this effect should be smaller in macroinvertebrates than in fish.

Variation in community composition may also be generated by species assorting along environmental gradients when dispersal is not sufficient to homogenize distributions (Leibold et al. 2004). The reduction in water velocity due to impoundment transforms river habitat into lentic habitat, with a concomitant change in biota (Kanehl et al. 1997; Gillette et al. 2005; Burroughs et al. 2010). The process of upstream pooling changes sediment transportation, filling in around large particles with fine sediments (Bednarek 2001) that may only be transported downstream during large flood events. This alters both the downstream habitats that rely on sediment and debris transportation (Liermann et al. 2012) as well as upstream fish and macroinvertebrates that require coarser substrates (Wood and Armitage 1997; Thomson et al. 2005). These environmental changes behind dams can displace lotic species via competition from lentic species, upstream migration to higher quality habitats, or both (Kanehl et al. 1997; Jackson et al. 2001; Burroughs et al. 2010). Overall, these habitat changes may cause shifts from natural community structure within impacted areas that reflect the sensitivity of individual organisms. While both fish and macroinvertebrate communities are likely to respond to environmental filtering, the low vagility of macroinvertebrate larvae within streams may make them more responsive to this metacommunity process.

Finally, community composition may be random, reflecting a lack of dispersal limitation or environmental filtering. Such neutral structuring (Leibold 2009) represents a null hypothesis for the system where there is no structuring of the community associated with environmental gradients or with distance. In this case, local communities would vary stochastically, unrelated to either distance or environment. Understanding how dams control metacommunity structure may directly suggest ways to ameliorate their impacts and predict the impacts of dam removal.

We used a metacommunity approach to understand dam impacts on community structure of two impounded rivers. This was done separately for two groups of organisms, fish and macroinvertebrates, which should respond to dams differently to provide an ecological contrast in susceptibility to impoundment. Community composition data across the two impoundments were used to address the following objectives: (1) to assess species richness, diversity, and biotic integrity of fish and macroinvertebrate communities in response to dams; (2) to assess fish and macroinvertebrate community structure responses to dams; and (3) to determine metacommunity drivers of fish and macroinvertebrate community structure. The overall objective of this study was to serve as a model to test the efficacy of dam removal in restoring the diversity and structure of river communities.

METHODS

Study area.—The Vermilion River in Danville, Illinois, is a tributary of the Wabash River, with a low-head dam, Danville Dam, approximately 35 km upstream from the confluence. The Vermilion River runs approximately 180 km in length and has a drainage area of 3,330 km^2 (Illinois Department of Natural Resources 2013). The Danville Dam was built in 1914 for industrial water usage but currently has no functional purpose (Illinois Department of Natural Resources 2013). Upstream from the dam (0.80 km) is the confluence of the North Fork Vermilion River, with a drainage area of 787 km^2 (Figure 1). This tributary also has a low-head dam, the Ellsworth Dam, 0.08 km upstream from the confluence. The Ellsworth Dam was constructed to replace a previous low-head dam around 1920 (Illinois Department of Natural Resources 2013). Both dams are classified as class III, or having low hazard potential for a fatal accident or substantial property damage (Illinois Department of Natural Resources 2013).

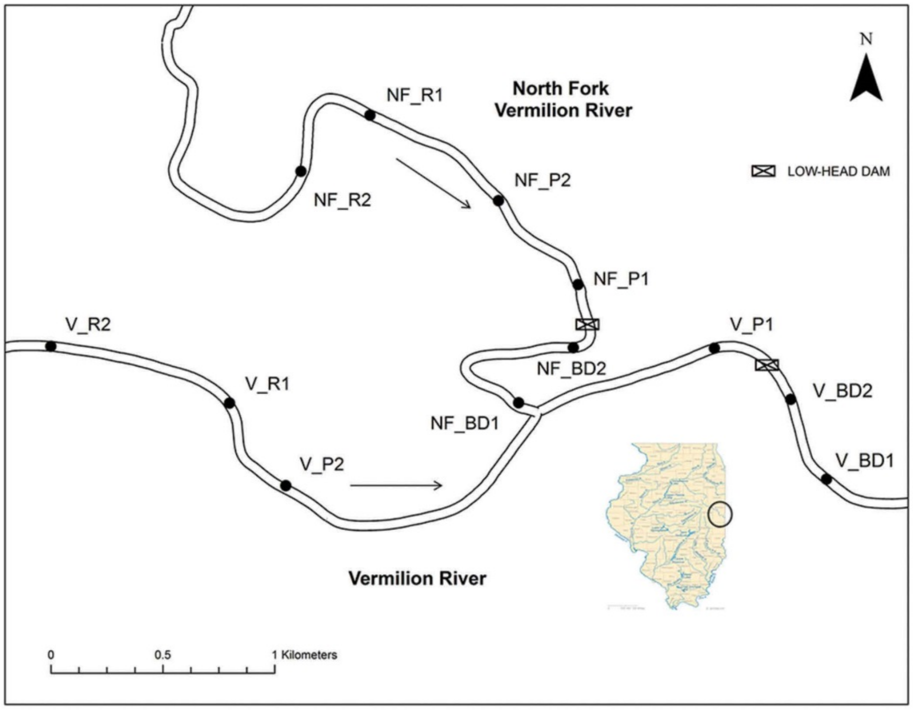

FIGURE 1. Map of the Vermilion River (V) and North Fork Vermilion River (NF). Sites are numbered by location: below dam (BD1, BD2), pool (P1, P2), and river (R1, R2).

Sampling design.—To assess the impacts of the dams on aquatic biota and stream habitat quality, fish and macroinvertebrate communities were sampled in October 2012 and 2013, in a series of 100-m-long sampling sites, with six in the North Fork Vermilion River (Ellsworth Dam) and six in the Vermilion River (Danville Dam; Figure 1). Each dam had two sites downstream of the dam and four sites upstream of the dam. The upstream dam sites consisted of locations directly upstream of the dam, the last 100-m-long section of the pool (pool sites), the first 100-m-long section of the river, and an upstream site (the farthest accessible upstream location–river sites). Thus, site codes are broken down by river location and site number (Figure 1). This sampling captured community composition both upstream and downstream of the dam (immediate impacts) and characteristics of sites upstream of each dam's impoundment influence.

Fish sampling used a multiple-gear approach to maintain capture efficiency across the variable conditions within the system. The multiple-gear approach was also used to keep consistency with previous Illinois Department of Natural Resources sampling (Illinois Department of Natural Resources 2013). Ellsworth Dam sites used direct current (DC) tow barge electrofishing with a 2,500-W generator and a five-person crew (three probe-netters and two extra netters). The entire wetted width at each site was electrofished in an upstream direction for a total of 30 min (Nielsen and Johnson 1983). No blocking seines were used given the large wetted widths (all sites >25 m) of the pool sites. Pool sites were determined by low flow, widest wetted widths (VR_P3-70m, NF_P3-33m) and depths greater than 1 m (Ohio EPA 2006). Vermilion River sites were deemed nonwadeable due to water depth (>1 m) and were sampled using one dipnetter on a DC electrofishing boat with a 4,000-W generator with two Wisconsin droppers (collapsible dropper–boom array). Each bank was shocked downstream to upstream for 15 min, for a total of 30 min/site. Two seine (9.14 × 1.22-m, 0.635-cm mesh) pulls were conducted for all Danville Dam sites at the nearest sandbar to ensure the collection of smaller fish the DC boat electrofishing may have missed. Cyprinids and fish less than 100 mm TL were euthanized and preserved in a 10% solution of formalin for identification in the laboratory. An index of biotic integrity (IBI) was calculated using the Illinois IBI calculator (Illinois Department of Natural Resources 2016). This software was created specifically for the state of Illinois and uses fish species abundance and river attributes (wetted width, slope, and region) to calculate integrity scores. These scores then categorize the quality of the site using fish species composition. The IBI scores are based off of Karr et al. (1986) and range from restricted (low) to unique (high).

Water conditions were collected using a YSI Professional Plus (YSI, Yellow Springs, Ohio) at all sites during all sampling periods measuring temperature (°C), dissolved oxygen (mg/L), pH, and conductivity (S/cm). Water samples were also collected at each location (river, pool, downstream of the dam) seasonally and brought back to the laboratory to measure suspended solids (g/mL), dissolved solids (g/mL), nitrogen (mg/L), phosphorus (mg/L), and ammonia (mg/L; American Public Health Association and American Water Works Association 1981). Preliminary analyses showed little variation among sites and seasons because of river stage on sampling dates. Therefore, these measures were dropped from all subsequent analyses. Velocity was recorded at three locations at each site with a Hach FH950 portable velocity meter, taking the surface velocity average of three measurements: thalweg of start, middle, and end of each site.

Habitat quality and macroinvertebrate communities were assessed at all wadeable sites ($N = 8$) using the Ohio qualitative habitat evaluation index (QHEI; Ohio EPA 2006). A modified QHEI protocol was used to assess habitat at all nonwadeable sites ($N = 4$). The QHEI protocol uses river width to determine the number of transects in each site. Each transect is then divided into intervals to sample the substrate–habitat type of the site. The overall percent of substrate–habitat type presence determines the quality of the site as poor, fair, good, or excellent (Ohio EPA 2006). A set of 20 jabs (dips) with a D-frame net was conducted based on the QHEI survey to sample substrate–habitats proportionally. Habitat assessment for the Vermilion upstream of the Danville Dam was done using a modified QHEI due to an increase in water depth. This was obtained by using the QHEI field sheet, determining habitat types by visual estimates. Macroinvertebrate sampling for these sites included a random set of 20 samples collected as the sites are nonwadeable. To ensure consistency, we conducted seven random jabs (D-frame net) on each bank side and six Ponar grabs (a dredge device used to sample benthic substrates) in the main channel. All macroinvertebrate samples were preserved in a 95% solution of ethanol for identification in the laboratory. Ethanol was drained, and the sample was spread over a tray divided into multiple quadrants (sample splitter). A subset of 300 macroinvertebrates was sampled using random subsamples and identified to the highest taxonomic resolution (family level in Chironomidae). Once identified, each taxa received a tolerance value (Merritt and Cummins 1996). A macroinvertebrate biotic integrity (MBI) was calculated by dividing the sum of the tolerance values by the total number of individuals sampled in the site (Hilsenhoff 1987). The MBI then categorizes the quality of the site based on the taxa present. Variation in metrics of fish (IBI) and macroinvertebrate (MBI) communities across sites and rivers were analyzed using a nested ANOVA in SAS version 9.3 (SAS 2006), including site as a factor nested within river. All analyses used an α of 0.05 to assess significance.

Community structure analyses.—Compositional variation among sites was assessed using nonmetric multidimensional scaling (NMDS) for fish communities (presence or absence) and macroinvertebrate communities (relative abundance of families). Presence–absence data were used for fish communities due to differences in gear types between rivers as a more conservative measure of composition that should minimize the influence of gear bias. This is in contrast to IBI, which included fish abundance data. Macroinvertebrate communities were analyzed using relative abundance data (% of total) as all sites were sampled with comparable effort. Following the ordination, we evaluated the statistical significance of compositional differences among sites and rivers using permutational multivariate ANOVAs (PERMANOVAs).

To evaluate the metacommunity structure of macroinvertebrate and fish communities, we first generated matrices of physical distance between sites (river channel length) and environmental dissimilarity between sites (based on substrate abundance, velocity, and water quality). Dispersal limitation and environmental filtering would be reflected by variation in community composition being associated with physical distance and environmental distance, respectively. Therefore, we also generated matrices of compositional distance for both macroinvertebrate and fish communities using Sorensen's dissimilarity index. Mantel tests were used to determine whether community structure was related to distance or environment for both fish and macroinvertebrates. As environmental characteristics are likely also associated with distance (closer samples are likely to be in the same habitat type), we followed the analysis of bulk patterns with partial Mantel tests to control for each factor. These tests assessed the effect of environmental similarity removing the influence of distance and the effect of distance removing the effect of environmental similarity to analytically isolate these drivers of metacommunity structure. Mantel tests, ordinations, and PERMANOVAs were conducted in PC-ORD version 6 (McCune and Grace 2002).

RESULTS

Habitat Quality

Dams appeared to affect the physical structure of habitats in both drainages. The Vermilion River experienced a drastic decrease in water velocity upstream of the dam, dropping from 0.24 m/s downstream to zero velocity immediately upstream of the dam (Figure 2). The North Fork Vermilion River also experienced a decrease in velocity in the pool

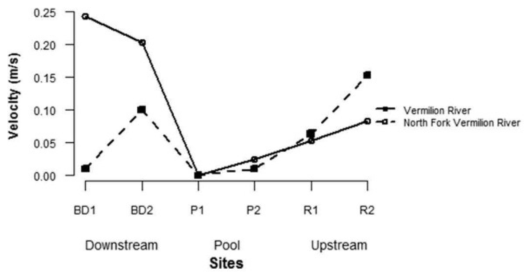

FIGURE 2. River velocity of the Vermilion River (solid) and North Fork Vermilion River (dashed) at base flow; ~3-ft gauge height from U.S. Geological Survey, Vermilion River near Danville, Illinois.

sites, but also decreased velocity in the most downstream dam site near the confluence (Figure 2). Substrate of the Vermilion River downstream the Danville Dam (V_BD1, V_BD2) consisted mainly of gravel and cobble, whereas upstream of the dam the substrate was dominated by sand (Figure 3A). The North Fork Vermilion River had a consistently high gravel proportion both downstream and upstream of the dam. Upstream of the Ellsworth pool there was an increase in cobble, whereas there was only appreciable sand at the lowest downstream dam site (Figure 3B). The QHEI scores ranged from 42 (poor) to 81 (excellent) for both rivers based on substrate and habitat abundance. The lowest rated site was V_P1, with a rating of 42, and is the closest pool site to the Danville Dam (Figure 4A). The highest rated site of 81 was the most upstream site in the North Fork Vermilion River, the site furthest from the Danville Dam (Figure 4A).

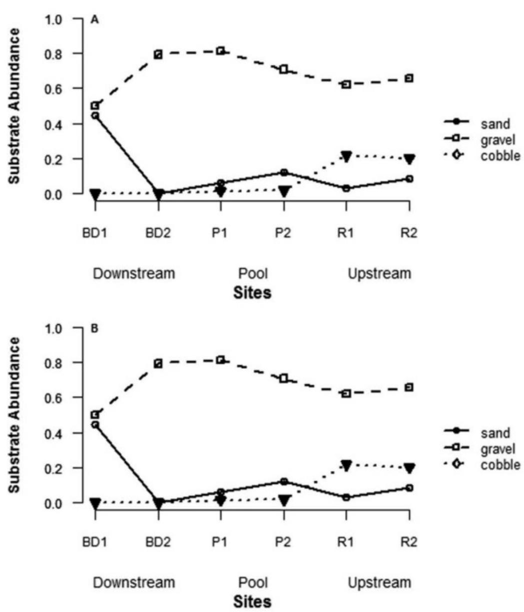

FIGURE 3. Distribution of substrate types across the dams in **(A)** the Vermilion River and **(B)** North Fork Vermilion. Top three substrate abundances are shown.

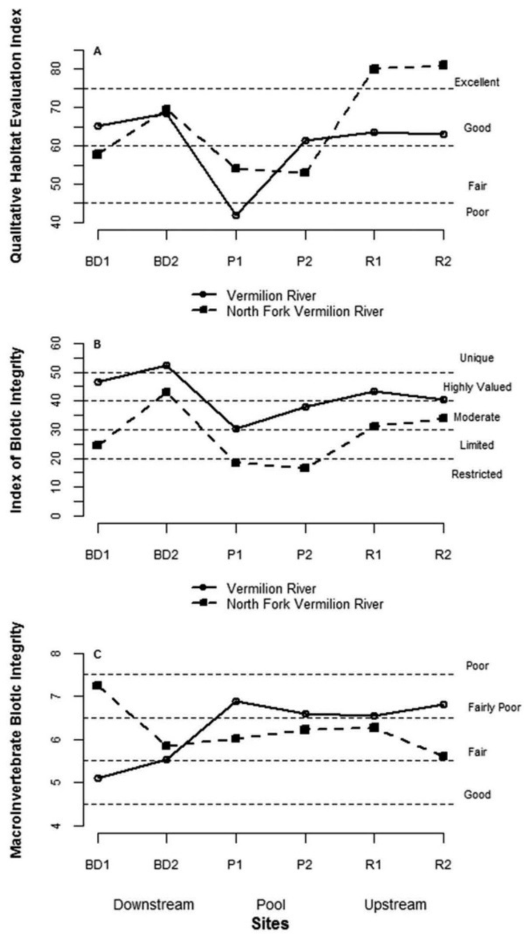

FIGURE 4. **(A)** Response of QHEI scores to the presence of dams on the Vermilion River (solid) and North Fork Vermilion (dashed). **(B)** Response of IBI scores to the presence of dams on the Vermilion River (solid) and North Fork Vermilion (dashed). **(C)** Macroinvertebrate biotic index scores of Vermilion River (solid) and North Fork Vermilion (dashed). Note the difference in *y*-axis scales due to the different indexes.

Fish

A total of 10,345 fish from 62 species were collected in the Vermilion River (53 species) and North Fork Vermilion River (41 species) in October of 2012 and 2013. Of the 62 species collected, there were two state endangered and two state threatened species (threatened: Eastern Sand Darter *Ammocrypta pellucida* and River Redhorse *Moxostoma carinatum*; endangered: Bluebreast Darter *Etheostoma camurum* and Bigeye Chub *Hybopsis amblops)*. Of the 13 families collected, distributions of Catostomidae (ANOVA: $F_{1,\ 5}$ = 12.23, P = 0.002), Centrarchidae (ANOVA: $F_{1,\ 5}$ = 23.83, P < 0.001), Clupeidae (ANOVA: $F_{1,\ 5}$ = 16.13, P = 0.008,) and Cyprinidae ($F_{1,\ 5}$ = 8.28, P = 0.010) varied significantly between rivers (Table 1). Overall, the Vermilion River exhibited higher IBI scores than the North Fork Vermilion River (Figure 4B), with both pool sites having the lowest IBI scores in the system (ANOVA: $F_{11,\ 12}$ = 13.06, P < 0.0001; Figure 4B). The IBI scores ranged from 16.5 (restricted) to 52.5 (unique). The highest score of 52.5 was immediately downstream of the Danville Dam, and the lowest score of 16.5 was at the upper end of the North Fork Vermilion River pool (Figure 4B).

Macroinvertebrates

A total of 7,002 macroinvertebrates from 109 taxa were identified in collections from fall 2012 and fall 2013. The Vermilion River had the lowest MBI downstream of the dam with higher, but quite consistent, MBI values upstream of the Danville Dam (Figure 4C). The North Fork Vermilion River had the highest MBI downstream, just upstream of the confluence with the Vermilion River, and the highest downstream of the dam. There was a similar increase in the MBI upstream of the dam as seen in the Vermilion River. The MBI patterns showed better differentiation among systems and significantly varied among locations between rivers (Figure 4C; ANOVA: $F_{2,\ 5}$ = 8.82, P = 0.0021). The best quality sites were in the Vermilion River downstream of the dam, with consistent increased MBI scores upstream of the dam. Analysis of North Fork Vermilion River MBI scores showed the most downstream sites below the dam; near the confluence of the Vermilion was the poorest rated site. Unlike the Vermilion River, the North Fork Vermilion River MBI increased in rating quality in the most upstream site (Figure 4C).

TABLE 1. Total catch of family by location within river; BD = below dam, P = pool, R = river.

	Vermilion River			North Fork Vermilion River		
Family	BD	P	R	BD	P	R
Atherinopsidae	85	36	7	0	0	0
Catostomidae	390	69	180	7	1	8
Centrarchidae	386	411	322	829	404	857
Clupeidae	117	40	152	31	0	0
Cyprinidae	1,838	490	1,647	910	23	351
Esocidae	0	3	0	0	0	0
Fundulidae	5	16	4	37	25	60
Ictaluridae	35	4	8	3	4	69
Lepisosidae	1	0	0	0	0	0
Moronidae	10	2	53	0	0	1
Percidae	18	0	4	55	4	111
Poeciliidae	1	67	22	73	1	14
Sciaenidae	43	0	1	0	0	0
Total	2,929	1,138	2,400	1,945	462	1,471

Fish Community Structure

Ordinations using NMDS revealed clear compositional separation between the rivers (Figure 5). The Vermilion River sites downstream of the dam and upper river sites had similar fish composition, whereas pool sites grouped on their own based on dominance of Gizzard Shad *Dorosoma cepedianum*. The separation of the North Fork Vermilion River sites in the NMDS was heavily dependent on *Etheostoma* spp., *Percina* spp., and *Noturus* spp. (Figure 5). These genera were found in high abundance in the upper river (NF_R1, NF_R2) and downstream of the Ellsworth Dam (NF_BD2) site. The pool sites of the North Fork Vermilion River also had the lowest abundances of fishes (Table 1). PERMANOVA verified river, location, and their interaction to be significant factors affecting fish communities (river: $F_{1,\ 18}$ = 15.20, P = 0.0002; location: $F_{2,\ 18}$ = 2.37, P = 0.006; river × location: $F_{2,\ 18}$ = 3.15, P = 0.0032).

Analyses of metacommunity structure showed there was an effect of habitat on fish community structure (Mantel test: t = 0.375, P = 0.002) but no significant effect of physical distance (t = 0.218, P = 0.104) on community structure. The association with habitat dissimilarity was positive, indicating that more similar physical habitats had more similar fish

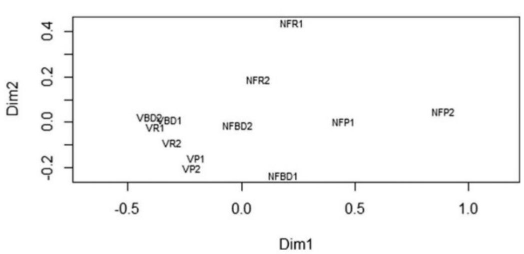

FIGURE 5. Nonmetric multidimensional scaling of fish assemblages using presence/absence data from both years pooled. There were two rivers sampled: the Vermilion River (R) and the North Fork Vermilion River (NF). Within each river there are three locations: below dam (BD), pool (P), and river (R). Within each location, there are two sites: (1) downstream and (2) upstream.

communities. Consistent with these results, the partial Mantel test controlling for distance still showed a strong effect of environmental dissimilarity (t = 0.291, P = 0.039), and the partial Mantel test of distance controlling for environment was nonsignificant (t = –0.001, P = 0.500).

Macroinvertebrate Community Structure

Patterns of macroinvertebrate community structure differed from fish communities in these sites. Ordination resulted in three distinct groups of invertebrate composition (Figure 6). Sites downstream of the dam on the Vermilion River were clustered and had high abundances of hacklegilled burrower mayflies *Potamanthidae* spp. Sites located upstream of the Danville Dam (Vermilion River), except NF_BD2, were clustered together as well (Figure 6). These sites had high abundances of Odonata, Chironomidae, and other Diptera. The remaining North Fork Vermilion River sites had large variation in macroinvertebrate communities. PERMANOVA reflected the complexity of compositional relationships: both river and the interaction of river and location were significant (river: $F_{1,\,18}$ = 5.30, P = 0.002; location: $F_{2,\,18}$ = 1.69, P = 0.112; river × location: $F_{2,\,18}$ = 3.37, P = 0.005). The metacommunity structure of macroinvertebrate communities differed from fish communities. Unlike the fish, macroinvertebrate communities were affected by distance (Mantel test: t = 0.407, P = 0.004) but not by environmental dissimilarity (t = 0.209, P = 0.089). The positive relationship indicated that locations further apart were more different in composition. Partial Mantel tests controlling for environmental conditions retained distance as a significant effect (t = 0.367, P = 0.010). Partial Mantel tests controlling for physical distance completely removed any signal of environmental dissimilarity on macroinvertebrate composition (t = –0.088, P = 0.728).

DISCUSSION

Both dams in this system act as dispersal barriers and create extensive pool reaches leading to a lentic habitat, with a concomitant decrease in water velocity and habitat quality as well as altered fish and macroinvertebrate communities. The reduction of velocity in these pools causes high sedimentation as well as reduced downstream transportation of different substrate types (Bednarek 2001; Connolly and Brenkman 2008). As with other studies, higher quality sites were located outside the pool reaches (Tiemann et al. 2004; Santucci et al. 2005; Butler and Whal 2010). The confluence of North Fork Vermilion River with the pool of the Vermilion River resulted in the lowest site (NF_BD1) being heavily silted and showing pool characteristics. This habitat structure indicates the pooling effect from the Danville Dam is being extended into the North Fork Vermilion River. The combination of substrate types and QHEI scores illustrate the physical impact of these dams in generating environmental alterations in habitat that may influence community composition.

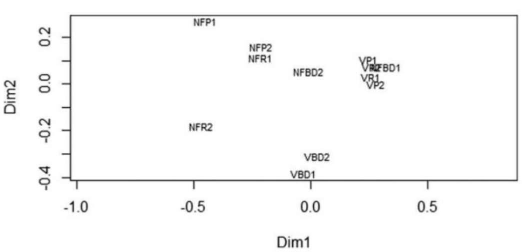

FIGURE 6. Nonmetric multidimensional scaling of sites based on relative abundance of macroinvertebrates. There were two rivers sampled: the Vermilion River (R) and the North Fork Vermilion River (NF). Within each river, there are three locations: below dam (BD), pool (P), and river (R). Within each location, there are two sites: (1) downstream and (2) upstream.

Fish Communities

The Vermilion River had the highest IBI scores and species richness in sites downstream of the dam. This is common in many impounded river systems due to the lack of efficient fish migration devices (Hammer and Linke 2003; Helms et al. 2011; Gardner et al. 2013). For example, several migratory species of Catostomidae (River Redhorse, Black Redhorse *M. duquesnei*, Golden Redhorse *M. erythrurum*, Shorthead Redhorse *M. macrolepidotum*, Quillback *Carpiodes cyprinus*, and Highfin Carpsucker *C. velifer*) were found in high abundances downstream of the dams. These species naturally exhibit constant movement behavior between pool, riffle, and run habitats, thus suggesting that the dams act as physical barriers for upstream movement (Lucas et al. 2001:169–170). In both rivers, almost 50% of the total catch occurred in the downstream dam sites. Removal of the dams should allow for greater abundances of these taxa to be found upstream (Catalano et al. 2007; Burroughs et al. 2010). The combination of the IBI scores and total fish abundance support the argument that these dams are acting as barriers to fish movement in the system (Kanehl et al 1997; Santucci et al. 2005; Wang et al. 2011). An existing fish ladder on the Danville Dam (Vermilion River) is highly degraded and has poor water velocity most of the year, and the Ellsworth Dam (North Fork Vermilion River) has no fish migration structure and often has no flow. Therefore, both dams effectively eliminate upstream and downstream connectivity except at high flow (Hastings et al. 2016).

While diversity and biotic indices of fish followed the expectation that dams act as physical barriers to fish, full compositional analyses did not support this. Biotic indices qualitatively valuate fish composition based on species tolerance, and diversity measures include information on the number of taxa only, regardless of identity. In contrast, analyses of full composition using NMDS are much better suited to address how assemblages are structured as they weigh all species equally and maintain species identity. Compositionally, there was a strong clustering of downstream-of-dam (V_BD1, V_BD2) and upper river sites (V_R1, V_R2) of the Vermilion River. Vermilion River downstream dam sites and upper river sites were similar in QHEI and had the highest velocities in the Vermilion River. The clustering of these sites in the NMDS reflected that fish communities were similar in the Vermilion River based on environmental similarity. The lack of water velocity and lower habitat quality in the Vermilion River pool sites displaced many species of fish to upstream or downstream habitats (Santucci et al. 2005). Sites in the North Fork Vermilion River had higher variability in velocity and QHEI, which appears related to their greater compositional dissimilarity. There were significantly fewer fish caught in the pool sites of the North Fork Vermilion River than in the sites immediately downstream of the dam and upper river sites. Overall, the North Fork Vermilion River is a smaller river with distinct pool, riffle, and run habitats, which may directly lead to heterogeneity in fish communities (Pyron and Taylor 1993).

The metacommunity structure of the fish community indicated that environmental filtering was the predominant factor determining the composition of local fish communities, as habitats more similar in substrate, water velocity, and water quality were more similar. This was true even when controlling for physical distance between sites, which is in sharp contrast to the expectation that dams should mediate local composition by reducing dispersal from neighboring habitats within the system (Martinez et al. 1994; Guenther and Spacie 2006; Nislow et al. 2011). The dominance of environmental filtering rather than dispersal limitation across dams indicates that there may be a sufficient mixing of fish communities during high flow events (Vehanen et al. 2005; Hastings et al. 2016), with a subsequent filtering of species along their environmental tolerances. This is not to say that all fish taxa do not respond to the low-head dams in this system, but that this is a minor component to community composition as a whole. The different pattern seen in fish IBI scores reflects the changes in dominance associated with lower quality habitats that such indices were designed to detect.

Macroinvertebrate Communities

Diversity and biotic indexes of macroinvertebrate communities followed the expectation that macroinvertebrates should primarily be affected by changes in habitat (Wood and Armitage 1997; Thomson et al. 2005). However, as was seen in fish communities, compositional patterns opposite to metacommunity predictions were found. For macroinvertebrates, physical distance was the main determinant of community structuring, even when controlling for environmental effects. The NMDS ordination clearly illustrates that sites were clustered based on the number of impoundments downstream. The furthest downstream sites were compositionally distinct from all sites upstream the Danville Dam. Likewise, sites upstream of the Ellsworth Dam were compositionally distinct from all other sites upstream of the Danville Dam, regardless of strong variation in habitat quality.

The ability of adult macroinvertebrates to fly across low-head dams for reproduction should alleviate the dispersal limitation necessary to generate local patch dynamics (Wallace and Anderson 1996; Hershey and Lamberti 2001; Karna et al. 2015). It is not clear why low-head dams may have impacted macroinvertebrates. As eggs and larvae largely move with current, the dispersal of macroinvertebrate early life stages should be primarily from upstream to downstream (Hershey and Lamberti 2001). Reduced velocities behind each dam may effectively filter out dispersing macroinvertebrates, reducing diversity and altering composition (Stanley et al. 2002). Environmental filtering may then reduce the ability of upstream, less-tolerant taxa to persist behind impoundments. Alternatively, the composition and dispersal of adult macroinvertebrates may be much more local, generating the spatial pattern of increasing dissimilarity with distance that was observed.

Implications of Metacommunity Structure for Dam Removal

The Vermilion River system is one of the highest quality systems in Illinois and is the index river for biotic integrity in the eastern region of Illinois. The slated removal of these two dams will remove both the local influence on pool structure and increase connectivity in the main channel and upstream habitats in the North Fork Vermilion River. The metacommunity structure described here suggests the mechanisms by which dams impact communities and therefore have utility in projecting the effects of dam removal. While we found patterning consistent with both environmental filtering and dispersal limitation, fish communities were impacted by the dams in fundamentally different ways than macroinvertebrate communities.

As fish communities were primarily influenced by environmental factors, the removal of dams and the reestablishment of natural river structure should rapidly be reflected in fish composition, diversity, and quality. Dam removal will immediately remove poorer quality pool habitats, leading to a decrease in lentic fish taxa and a concomitant increase in IBI. This recovery is likely to be facilitated by enhanced movement of the barrier-susceptible species that we observed (Brenkman et al. 2008; Burroughs et al. 2010), particularly for sport fish (Hill et al. 1994; Kanehl et al. 1997). For example, Smallmouth Bass *Micropterus dolomieu* requires clear water quality, gravel-rocky substrates, and moderate-to-fast water velocities (Smith 2002). A total of 93 Smallmouth Bass were captured, with 51.6% captured downstream of the dams, 14% in pools, and 34.4% sampled in upper river sections. Similarly, removal of the dams may allow endangered and threatened species such as the Bigeye Chub, Bigeye Shiner *Notropis boops*, Bluebreast Darter, Eastern Sand Darter, and the River Redhorse to unite with upstream populations and increase the effective population size (American Rivers 2002).

Removal of the dams will likely have a positive impact on macroinvertebrate communities in the long term. However, short-term negative effects may occur from the release of fine sediments accumulated upstream of the dam (Gray and Ward 1982; Thomson et al. 2005) that will fill interstitial spaces needed by some aquatic macroinvertebrates (Wood and Armitage 1997). Sites located downstream of the dams will be affected by the sediment release, causing fish to disperse to higher quality habitats (Catalano et al. 2007; Burroughs et al. 2010). The long-term effects of dam removal should increase lotic taxa and decrease lentic taxa in the former pool habitats (Bushaw-Newton et al. 2002; Stanley et al. 2002; Thomson et al. 2005), leading to an overall increase in the biotic integrity of the Vermilion River and the North Fork Vermilion River. The importance of physical distance over local environmental factors in determining macroinvertebrate composition may disappear following dam removal if the dams were functioning as sinks for early life history stages. If distance decay patterns do not change, this suggests that dispersal is limited for some other reason than the presence of dams.

Applying a metacommunity perspective to this impounded system allowed us to isolate drivers of community composition and revealed fundamental differences in how these two communities were structured. Furthermore, this approach allowed us to isolate unexpected barrier effects on macroinvertebrates and the greater importance of environmental filtering for fish. These effects suggest that both processes may be occurring in unimpounded systems where environmental and spatial gradients likely occur over larger areas.

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NOTE

When to sample: flow variation mediates low-head dam effects on fish assemblages

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Low-head dams are a primary source of anthropogenic disturbance to river systems. They have the ability to change rivers from lotic to lentic habitats, affect sediment transportation, connectivity, water quality, linkages with wetlands and the quality of in-stream and riparian habitats. These changes can effect fish community structures and have the potential to alter the success of organisms in the system. However, there is no standard sampling protocol to assess dam impacts under varying flow regimes. The Vermilion River and its tributary, the North Fork Vermilion, are both impacted by low-head dams creating lentic habitats within each system. In October 2012 and May 2013, fish assemblages were sampled using direct current (DC) electrofishing at a total of 12 sites. Community composition at base flow responded strongly to both dams and differed between the two drainages. In sharp contrast, there was no effect of dams or differences between rivers during high flow. To adequately assess dam impacts on fish assemblages, we recommend sampling after base flow has been established. Sampling at high flow will reflect the homogenization of habitats and fish assemblages.

Keywords: dam removal; fish assemblage; flow variation; metacommunity structure; sampling protocols

Anthropogenic forces are the main disturbances for waterways globally and include dams, spillways, channel modification, industrial outflow and agriculture. Ecologically, dams change habitats from lotic to lentic, affect sediment transportation, water quality, connectivity and the quality of in-stream habitats (Poff & Hart 2002; Nilsson et al. 2005; Guenther & Spacie 2006). The generation of new habitat types within impounded reaches increases the performance of species that would otherwise be rare in lotic systems, leading to distinct fish assemblages in the pools that form behind dams (Gillette et al. 2005; Santucci et al. 2005; Butler & Wahl 2010).

Dams can affect metacommunity composition by altering the movement of fish species across the dam. Within river systems, dispersal is critical for community stability as it allows species to migrate to new habitats, follow shifting food sources and integrate with other populations. Dams with improper fish passages cause species below the dam to be excluded from upstream reaches and eliminate passage to quality habitats (Burroughs et al. 2010). The combined abiotic and biotic effects of dams can greatly influence the success of individual species by changing habitat, food web structure, reproductive success and migration (Nislow & Letcher 2011). The aggregate alteration of fish movement and habitat structure can therefore dramatically affect fish community structure.

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However, fish community structure also changes seasonally based on life history differences and habitat variability and accessibility (Taylor 1996, 2000). High flows can allow different fish species to access habitats or may even alter preexisting habitats allowing for utilization by different fish species (Taylor et al. 2006). Therefore, shifts in seasonal discharge may mediate the impacts of impoundments on fish communities.

Impacts to fish communities are one of the major justifications for the removal of impoundments (Helms et al. 2011). However, there is no standard sampling protocol that defines when fish surveys to assess dam impacts should be conducted. This paper aims to determine whether flow alters the patterns seen across impoundments and whether this can inform when to sample assemblages.

The Vermilion River in Danville, IL, USA is a tributary of the Wabash River with a low-head dam, Danville Dam, approximately 35 km upstream from the confluence. The Danville Dam was built in 1914 for industrial operations, is classified as a class III low-head dam, and currently has no functional purpose (Illinois 2013). Half a mile upstream from the dam is the confluence of the North Fork Vermilion River (Figure 1). This tributary also has a low-head dam, Ellsworth Dam, 0.08 km upstream from the confluence. The Ellsworth dam was constructed to replace the original low-head dam around 1920 (Illinois 2013). It is also classified as a class III low-head dam (Illinois 2013). Both of these dams act as barriers to fish movement at base flow (Figure 2). During spring floods, the Ellsworth Dam is often submerged allowing for connectivity within the North Fork. The Danville Dam can also become submerged, but only during 10-year floods (T. Thomas, personal observation). These spring floods may temporarily restore connectivity and reduce the effects of the dams on the stream biota.

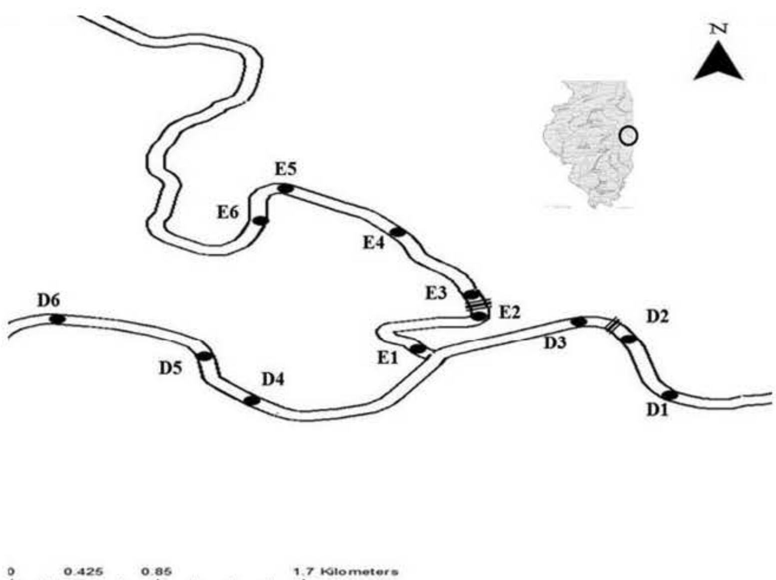

Figure 1. Vermilion (D) and North Fork Vermilion River (E) sampling sites. Below dam sites (1,2), pool sites (3,4) and upper river sites (5,6). The Danville Dam is located between D2 and D3 and is 67.25 m wide and 3.35 m high (−87.631691, 40.122256). The Ellsworth dam is located between E2 and E3 and is 27.43 m wide and 1.83m high (−87.638788, 40.123888).

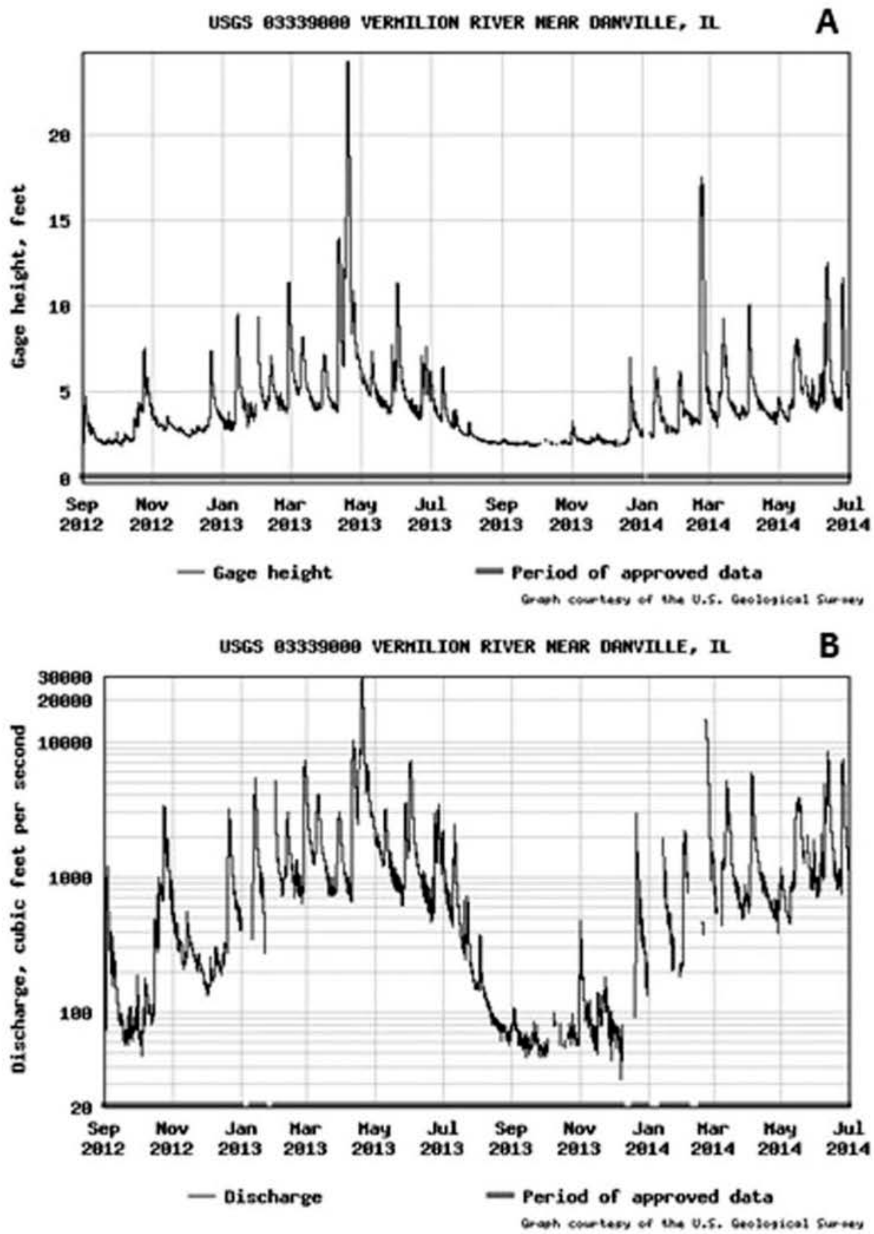

Figure 2. (A) Hydrograph and (B) discharge of the Vermilion River from United States Geological Survey. Base flow is observed from the end of July 2013 to middle of December 2013.

To assess impacts of the impoundments on fish assemblages during different flow regimes, sampling was conducted sequentially during October 2012 (fall – base flow) and May 2013 (spring – high flow). Fish were sampled in 12, 100-m sections of river. Six were located in the North Fork Vermilion (Ellsworth Dam sites) and six in the Vermilion (Danville Dam sites; Figure 1). For each dam, sampling consisted of two sites below the dam, two sites in the pool (directly above the dam and the last 100 meters of the pool) and two river sites (the first 100 meters of the river above the pool and the farthest accessible upstream location.

Ellsworth Dam fall sampling was conducted using direct current (DC) barge electrofishing with a 2500 watt generator. Each site was electrofished by a five-person crew for a total of 30 minutes beginning downstream and moving upstream. Danville Dam was sampled using DC boat electrofishing with a 3000 watt generator with two Wisconsin droppers for a total of 30 minutes with one netter across the entire area. This methodology reflects the larger size of this channel. Two bag seine (9.14 m × 1.22 m, 0.635 cm mesh) pulls were conducted at the Danville Dam sites at the nearest sandbar to ensure collection of smaller fish which DC boat electrofishing often misses. Seine pulls were conducted at the nearest sandbar located near the center of the electrofishing site. Spring sampling protocols had to be adjusted due to changes in river conditions; both rivers were sampled using DC boat electrofishing with a 3000 watt generator. These samples were supplemented with two mini-fyke nets (3.0 mm mesh, lead 4.5 m × 0.6 m, cab 3 m × 0.6m × 1.2 m) at each seine site for 24 hours to collect smaller fish. Though shifts in methodology restrict our ability to directly compare across rivers at base flow and between flow regimes, our focus is on within stream changes associated with dams in each period.

A total of 54 fish species were collected during fall and 56 species during spring. Of these, 10 species were only found during fall and 12 species during spring. The species found only at high flow were larger riverine fishes, three native buffalo species (*Ictiobus spp.*), three species of gar (*Lepisosteus spp.*) and the non-native silver carp (*Hypophthalmichthys molitrix*). Catostomidae abundances varied dramatically between seasons within pool sites. Abundances in Vermilion pool sites increased from < 1.0 to 13.7% of the community (7–47 individuals) and from 0.0 to 5.0% (16 individuals) in North Fork pools. Also, *Moxostoma* species were not captured anywhere within North Fork sites during fall but found in all sites during spring. The presence of *Moxostoma* in the North Fork in the spring indicates there is suitable habitat for spawning and fish can disperse upstream when the dam is submerged (Kwak & Skelly 1992). Overall, there were large seasonal changes in composition, due to an increase in river connectivity and a decrease of pool habitat.

To examine spatial patterns of fish community composition, a hierarchical cluster analysis was conducted for each sampling using a presence/absence matrix in PCORD 6 (McCune & Grace 2002). A presence/absence matrix was used to minimize gear bias due to differences in sampling techniques, a common issue with dams as they dramatically change structure. Community composition at base flow showed strong influences of both dams on fish assemblages and revealed compositional differences between the two drainages (Figure 3(A)). In sharp contrast, there was no separation in community composition between rivers or sites during high flow (Figure 3(B)). This pattern was also observed when using non-metric multidimensional scaling (NMDS) ordinations (not shown). At base flow there was compositional structure associated with both dams and rivers, but during high flow NMDS found no structure in the data.

These analyses show how fish assemblage responses to dams are mitigated by flow. The separation of sites at base flow show strong effects of the dams in the system and

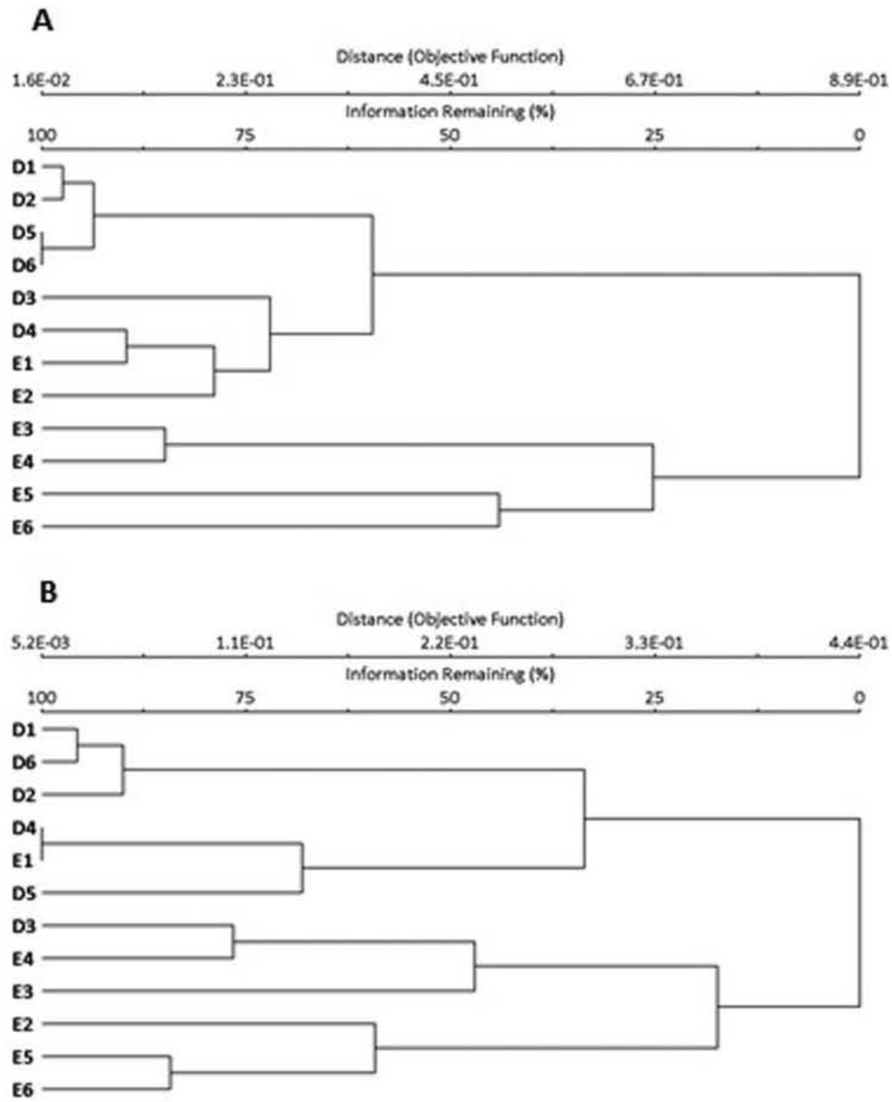

Figure 3. Cluster analysis of (A) fall 2012 and (B) spring 2013 communities using species presence absence.

also show relationships among sites. Below dam and upper river sections of the Vermilion were similar (Figure 3(A)), revealing a spatially limited dam impact and a large shift in composition caused by the pool. Pool sections of the Vermilion were also compositionally similar to the below dam sites on the North Fork, reflecting their connectivity. In contrast, fish composition during high flow did not vary between the two drainages or across the dams despite the consistent sampling methodology. This suggests the impact of dams is greatest at base flow, whereas the communities mix at high flow. Seasonal variability in fish community composition is likely caused by greater fish movement during increased discharge.

As a second measure of discharge-related changes in fish community structure, we used Mantel tests to relate physical distance (stream length) between sites to compositional dissimilarity (Sorensen's distance). These tests showed that sites located further apart were overall less similar in family composition ($p = 0.003$, $t = 2.914$) and species composition ($p = 0.002$, $t = 3.034$) at base flow. This suggests distance-affected assemblage structure (Thompson & Townsend 2006; Ruiz-Gomez et al. 2008). The compositional similarity of downstream and river sections of the Vermillion shown in the cluster analysis was not sufficient to disrupt this overall pattern. In contrast, analyses at high flow showed no pattern for either family ($p = 0.930$, $t = 0.0875$) or species ($p = 0.210$, $t = 0.1745$) composition, showing mixing of fish assemblages during increased discharge. Together, these results indicate the timing of sampling relative to flow regime may have profound influences on the ability to detect dam impacts on fish assemblages.

Studies documenting the biological effects of dams are becoming more common due to the push to remove many low-head dams (Gillette et al. 2005; Santucci et al. 2005; Slawski et al. 2008). The dams in this system are slated to be removed based on safety concerns but also because of impact on fish assemblage. The Vermilion River system is one of the highest quality river systems in Illinois and is used as the reference site for the Illinois eastern region for indices of biotic integrity. There are few challenges to the system outside of the effects of the dams, reflected in the species present. Spring time floods increased connectivity allowing access to fishes, such as buffalo species (*Ictiobus spp.*), as well as multiple redhorse species (*Moxostoma spp.*).Whether homogenization at high flow is driven by downstream fish migrating above the dam or upstream fish moving downstream is not clear. Nor is it clear whether this mixing at high flow is sufficient to ensure gene flow across dams. The population level implications of this temporal connectivity are a critical conservation issue. To adequately assess dam impacts on fish assemblages, sampling protocols must account for seasonal fluctuations in both rivers and the communities within them. To adequately document dam impacts on fish assemblages, sampling must occur once base flow has been re-established and the temporary mixing of communities has abated. Sampling during high flow may result in the spurious conclusion that a dam is having no impact on stream fishes. These results also suggest that more work is needed to determine whether low-head dams are effectively isolating populations or whether high flow events allow sufficient contact between upstream and downstream populations.

Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental data

Supplemental data for this article can be accessed http://dx.doi.org/10.1080/02705060.2015.1079560.

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Effects of Lowhead Dams on Freshwater Mussels in the Vermilion River Basin, Illinois, with Comments on a Natural Dam Removal

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ABSTRACT

We sampled freshwater mussels at 12 sites centered around three lowhead dams in the Vermilion River basin (Wabash River drainage) to address their effects on the freshwater mussel fauna and to obtain baseline data prior to their removal. Compared with reference sites, impounded areas and plunge zones had lower mussel abundance and extant species richness. We also examined literature accounts and museum collections to determine species distributions in the basin and compared those data to locations of the three dams and location of the former Homer Park Dam, which was removed over 50 years ago. Two species, Yellow Sandshell (*Lampsilis teres*) and the state-threatened Black Sandshell (*Ligumia recta*), are now found only downstream of the Danville Dam. Pimpleback (*Amphinaias pustulosa*) and Mapleleaf (*Quadrula quadrula*), which was found only downstream of the Homer Park Dam prior to 1950, has expanded its range upstream since the dam was removed. Data collected during this study contributes insights into the effects of lowhead dams on freshwater mussel abundance and species richness in Midwestern streams, and will be used as a baseline to compare to future post-dam removal collections.

INTRODUCTION

Freshwater mussels (Bivalvia: Unionoida) are among the most imperiled groups of organisms in the world (Bogan 1993; Williams et al. 1993; Lydeard et al. 2004; Strayer et al. 2004). In North America, nearly 74% of the approximate 300 species are listed as endangered, threatened or in need of conservation status. Anthropogenic disturbances resulting in habitat fragmentation and environmental degradation are among factors affecting mussels (Haag 2012).

Impoundments are one of the major sources of anthropogenic disturbances in streams and affect river systems in a myriad of ways (Baxter 1977). Conversion of lotic habitats to lentic habitats by dams has cascading effects on the stream's hydrogeomorphology, which includes modified flows regimes, altered physicochemical parameters, increased siltation upstream from dams, and scoured substrates downstream from dams (Tiemann et al. 2004; Maloney et al. 2008; Csiki and Rhoads 2010; Csiki and Rhoads 2014). Resulting effects on native mussels are equivocal, but include reduced species richness and abundance, fragmented populations, restricted distributions, and alterations of host-fish assemblages (Baker 1922; Watters 1996; Vaughn and Taylor 1999; Dean et al. 2002; Tiemann et al. 2004; Tiemann et al. 2007b; Galbraith and Vaughn 2011).

The objective of this study was to investigate if lowhead dams (< 4 m in height) have affected the freshwater mussel fauna in the Vermilion River basin (Wabash River drainage), Illinois. Two of the three dams we investigated are scheduled for demolition, and data from this study will be used to assess the baseline condition of the mussel fauna prior to removal. These data also will be used during post-dam removal monitoring, as mussel populations are likely to take decades to colonize previously impounded reaches (Kappes and Haase 2012).

STUDY AREA

The Vermilion River basin (Wabash River drainage) drains nearly 4,000 km^2 of eastern Illinois and western Indiana. The mainstem and its three largest tributaries (Salt Fork, Middle Fork, and North Fork) are relatively free-flowing except for four dams in Danville, Vermilion County, Illinois (Figure 1): Danville Dam (or Vermilion Dam) on the mainstem Vermilion River; Ellsworth Park Dam on the North Fork, 1.8 km upstream of the Danville Dam; Aqua Illinois Dam (or Waterworks Dam) on the North Fork 3.8 km upstream of the Ellsworth Park Dam; and Lake Vermilion Dam on the North Fork, 4.1 km upstream of the Aqua Illinois Dam (Tiemann 2008; Csiki and Rhoads 2014). Other human-induced modifications in the basin include draining of wetlands, dredging of streams, pollution from agriculture and industrial sources, and development of floodplains (Baker 1922; Smith 1968; Page et al. 1992; Larimore and Bayley 1996). Despite these disturbances, the Vermilion River basin remains one of the highest quality and biodiverse stream systems in Illinois (Smith 1968; Page et al. 1992) with 45 species of freshwater mussels (Tiemann et al. 2007a; Stodola et al. 2013) and over 100 species of fishes (Retzer 2005; Tiemann 2008) known from the basin. Although the watershed is primarily agriculture, most stream reaches have largely intact riparian zones and sand, gravel, and cobble substrates (Smith 1968; Page et al. 1992).

METHODS

The study design is similar to that of Dean et al. (2002) and Tiemann et al. (2004). We sampled 12 sites centered around three lowhead dams (Aqua Illinois, Ellsworth Park, and Danville) to assess effects of lowhead dams on the freshwater mussel fauna (Figure 1). Around each dam were site-types, which included reference sites, the impounded area, and the plunge zones. Reference sites were free-flowing (to 0.5 m/s during base flow), were 0.5-1.0 m in depth, and predominantly contained gravel/pebble substrates; these areas were outside the zone of direct dam influence on flow and we deemed these sites to be appropriate surrogates for presently free-flowing portions of the Vermilion River. Impounded areas were located <0.25 km upstream from the dam, had no flow, were 0.5-2+ m in depth, and primarily contained sandy substrates with small pockets of silt. Plunge zone sites were located <0.1 km downstream from

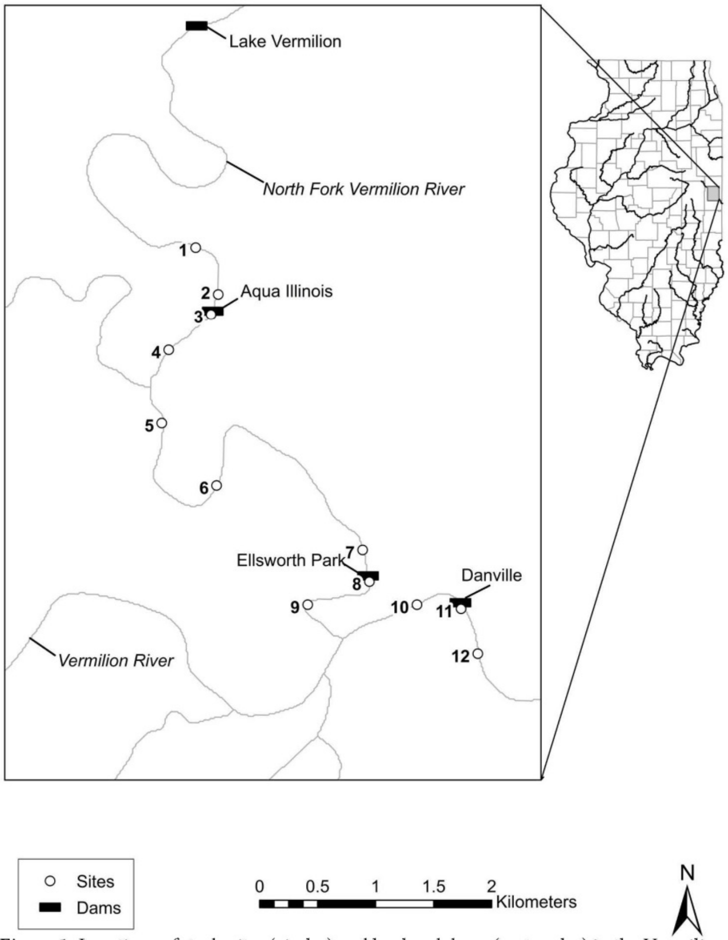

Figure 1. Locations of study sites (circles) and lowhead dams (rectangles) in the Vermilion River basin, in Danville, Vermilion County, Illinois.

the dam, were 0.5-2 m in depth, and had a diverse substrate composition, including gravel/pebble and cobble.

Live freshwater mussels and valves of dead specimens were collected by hand grabbing (e.g., feeling the substrate with one's hands) for four person-hours at each of the 12 sites during the summer of 2014. All sites were <100 m in length and efforts were made to cover all available habitat types present at a site including riffles, runs, pools, slack water, and areas of differing substrates. Individuals were identified before being returned to the site. Shell material was classified as fresh-dead (periostracum present, nacre pearly, and soft tissue may be present) or relict (periostracum eroded, nacre faded, shell chalky) based on condition of the best shell found. A species was considered extant at a site if it was represented by live or fresh-dead shell material. Voucher specimens of all species were deposited in the Illinois Natural History Survey (INHS) Mollusk Collection, Champaign, and scientific names follow Graf and Cummings (2007), except for recent taxonomic changes to the gender ending of species in the genus *Toxolasma*, which follow Williams et al. (2008).

Data were pooled for analysis at the site-type level (Tiemann et al. 2004; Tiemann et al. 2007b). We calculated an index of freshwater mussel abundance (number of individuals per hour; henceforth referred to as abundance) and extant species richness (number of species collected alive or as fresh-dead). Analysis of variance (ANOVA) was conducted to test the hypothesis that the assemblage varied by site-type, and Tukey's studentized range test was used for pairwise comparisons among site-types (Zar 1999).

We reviewed pertinent literature (e.g., Baker 1906; Zetek 1918; Baker 1922; Van Cleave 1940; Matteson and Dexter 1966; Suloway et al. 1981b; Cummings and Mayer 1997; Szafoni et al. 2000; Tiemann et al. 2007a; Stodola et al. 2013) and examined museum specimens and associated data (e.g., Academy of Natural Sciences at Drexel, Philadelphia; Chicago Academy of Science; Carnegie Museum of Natural History, Pittsburgh; Field Museum of Natural History, Chicago; Florida Museum of Natural History, Gainesville; the now combined Illinois Natural History Survey and University of Illinois Museum of Natural History, Champaign; Illinois State Museum, Springfield; Museum of Comparative Zoology, Cambridge, MA; Ohio State University Museum of Zoology, Columbus; and University of Michigan Museum of Zoology, Ann Arbor) to determine species distributions within the Vermilion River basin. A species was considered extant at a site if it had been collected there since 1970 (Cummings and Mayer 1997; Tiemann et al. 2007a). To recognize whether dams affected unionid distribution, we determined presence of a given species and compared those data to locations of the lowhead dams in the Danville areas as well as the former Homer Park Dam (e.g., Watters 1996; Tiemann 2007b). The Homer Park Dam was a lowhead dam on the Salt Fork that Baker (1922) stated was "an effective barrier" to the upstream migration of 12 species of mussels. This dam, which was near the Illinois Route 49 bridge north of the village of Homer, washed away between 1939 and 1958 (Matteson and Dexter 1966).

RESULTS

Freshwater mussel abundance ($F = 12.86$; $df = 2, 9$; $P = 0.002$) and extant species rich-

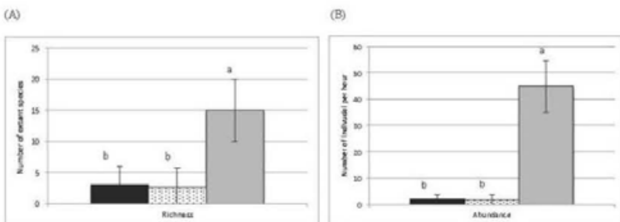

Figure 2. Mean freshwater mussel abundance (A) and extant species richness (B) with standard deviation bars by site-type from the Vermilion River basin, in Danville, Vermilion County, Illinois. Impounded areas are first column (black), followed by plunge areas (white with speckling), and reference areas (gray). The lowercase letters in the lowest panel indicate significant groupings according to Tukey's test.

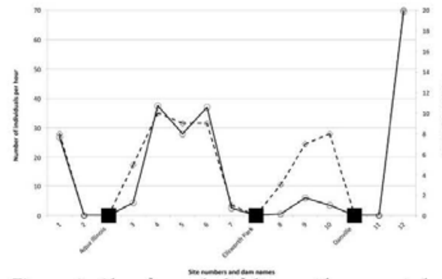

Figure 3. Abundance (solid lines with open circles) and extant species richness (dashed line with open diamonds) of freshwater mussels by site and the location of dams (solid squares) in the Vermilion River basin, in Danville, Vermilion County, Illinois. Figure 1 lists the locations of sites and dams. Sites progress from upstream (site 1) to downstream (site 2).

ness ($F = 6.78$; $df = 2, 9$; $P = 0.02$) differed significantly among site types. Tukey's test revealed that both abundance and extant species richness were greater at reference sites than at either impounded areas or plunge zones. Reference sites had abundances that varied from 26.8 to 69.5 individuals per hour (mean = 37.67), whereas impounded areas varied from 0 to 3.5 (mean = 2.00) and plunge areas varied from 0 to 4.3 (mean = 1.63) (Figure 2; Figure 3). Extant species richness varied from 8 to 20 (mean = 11.8) in reference areas compared to 0 - 8 (mean = 3.0) in impounded areas and 0 to 5 (mean = 2.7) in plunge zones (Figure 2; Figure 3). It is important to note that of the 8 extant species at Site 10 (the Danville Dam impounded area), only one was alive and the remaining were fresh-dead and could have washed downstream.

Examination of literature (n = 14 articles) and museum data (n >4,000 specimens) from the Vermilion River basin suggests that the Danville Dam (downstream most dam in the basin) appears to now limit the upstream distribution of five species. Three species, Threehorn Wartyback (*Obliquaria reflexa*), Hickorynut (*Obovaria olivaria*), and Fawnsfoot (*Truncilla donaciformis*), have records only downstream of the Danville Dam, and we excluded them from this analysis. All three species are considered a large river species that occasionally are found in the lower end of medium-sized streams (Cummings and Mayer 1992; Cummings and Mayer 1997; Tiemann et al. 2007a; Stodola et al. 2014). Hickorynut has never been very abundant in the lower Vermilion River mainstem (INHS Mollusk Collection), thus we do not expect it to be common upstream of the dams. However, both Threehorn Wartyback and Fawnsfoot are expanding their ranges across Illinois and are colonizing new basins (Tiemann et al. 2007a). Threehorn Wartyback and Fawnsfoot were recorded for the first time in the Vermilion River basin in 2006 and 2007 (INHS Mollusk Collection), respectively, thus they may eventually migrate upstream of the dam.

Based upon 14 records in the Vermilion River basin, Yellow Sandshell (*Lampsilis teres*) occurred as far upstream in the Salt Fork as the former Homer Park Dam near Homer (INHS 36874) and as far upstream in the Middle Fork as the US Highway 150 bridge near the village of Oakwood (INHS 37235) (Figure 4). Twenty-two records exist for Black Sandshell (*Ligumia recta*) in the Vermilion River basin, including records as far upstream in the Middle Fork as the Vermilion County Road 900E bridge (= "Higginsville Bridge") near the village of Collison (INHS 14463) and as far upstream in the Salt Fork as Vermilion County Road 130E bridge near the village of Homer (INHS 45733) (Figure 4).

Examination of literature and museum collection holdings suggested that, of the 12 species listed by Baker (1922), only Pimpleback (*Amphinaias pustulosa*) and Mapleleaf (*Quadrula quadrula*) have expanded their ranges upstream of the former Homer Park Dam. However, of the remaining 10 species, seven are imperiled – Round Hickorynut (*Obovaria subrotunda*) is extirpated from Illinois, Clubshell (*Pleurobema clava*) is federally-endangered and was considered only extant in the North Fork, Purple Lilliput (*Toxolasma lividum*) is state-endangered and extirpated from the Salt Fork, Wavyrayed Lampmussel (*Lampsilis fasciola*) is state-endangered and found throughout the Vermilion River basin, Purple Wartyback (*Cyclonaias tuberculata*) is state-threatened and found throughout the basin, Monkeyface (*Theliderma metanevra*) is listed as a species in greatest-need-of-conservation and found throughout the basin, and Ellipse (*Venustaconcha ellipsiformis*) is extirpated from the basin. These seven species, in addition to Yellow Sandshell referenced above, all have experienced substantial range reductions in the Vermilion River basin since Baker's (1922) study and, if still extant in the basin today, are present in low numbers (Stodola et al. 2013; INHS Mollusk Collection); therefore, we concluded that these species are not representative of the success of recolonization following dam removal. Two species, Pistolgrip (*Tritogonia verrucosa*) and Mucket (*Actinonaias ligamentina*), are currently extant in the Salt Fork, although in low abundances, and appear extant downstream of the former Homer Park Dam but not upstream of it (Stodola et al. 2013; INHS Mollusk Collection).

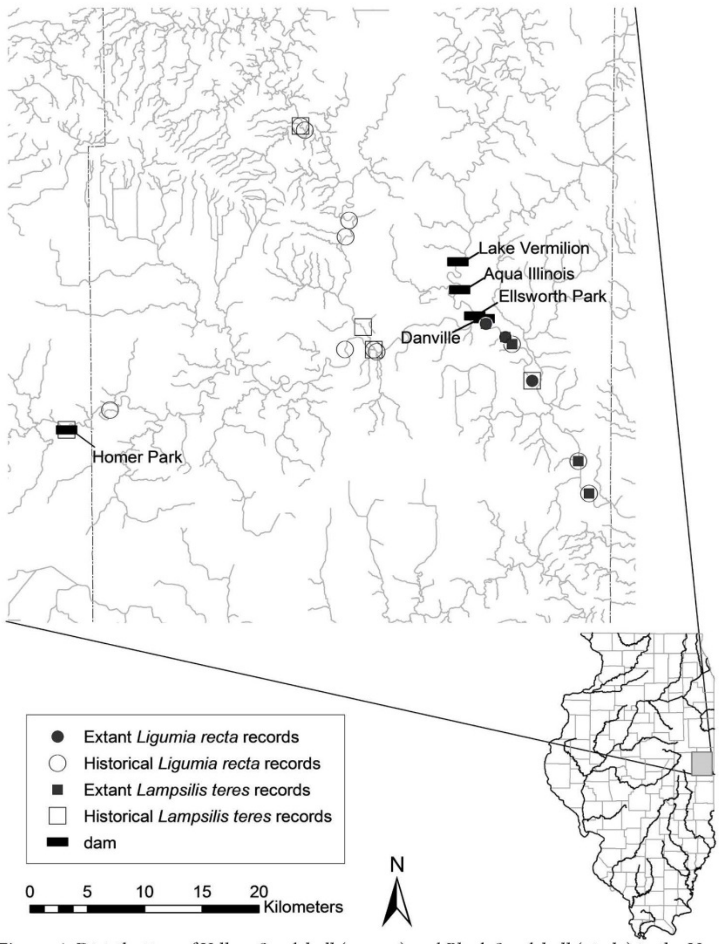

Figure 4. Distribution of Yellow Sandshell (square) and Black Sandshell (circle) in the Vermilion River basin (Wabash River drainage). Solid symbols denote sites where specimens have been found extant since 1970, whereas open symbols are historical records. Solid rectangles are locations of dams and include Lake Vermilion dam, as well as Aqua Illinois, Ellsworth Park, and Danville lowhead dams.

DISCUSSION

The significant differences in mussel abundance and extant species richness observed among site-types are likely the result of degraded habitats in the impounded areas and plunge zones. Csiki and Rhoads (2014) measured geomorphologic parameters in the Vermilion River basin around Ellsworth and Danville dams, and reported that although Ellsworth and Danville dams have minimal fine-sediment trapping ability, substantial fine sediment accumulation was documented in both impoundments. Freshwater mussels usually prefer free-flowing environments with clean heterogeneous substrates (Cummings and Mayer 1992; Williams et al. 1993; Watters et al. 2009; Haag 2012). In impounded areas, reduced water velocities allow silt and debris to accumulate and smother sand and gravel substrates (Tiemann et al. 2004; Csiki and Rhoads 2014), thus creating habitat unsuitable for most mussel species (Baker 1922; Suloway et al. 1981a; Dean et al. 2002; Tiemann et al. 2007b).

Dams also can affect downstream habitat directly through physical stresses (e.g., scouring). Counter to some studies from the southeastern United States that suggest dams enhance conditions for mussel growth in downstream reaches by stabilizing substrates downstream from the impoundment (Gangloff 2013, and references therein), studies from the Midwest suggest that dams increase scouring of substrates immediately downstream from the impoundment (Tiemann et al. 2004; Csiki and Rhoads 2014). Midwestern streams often flow through fluvial and glaciofluvial deposits that are easily erodible, and tailwaters frequently scour substrates in an attempt to obtain a water flux – sediment load equilibrium (Kondolf 1997). In the Vermilion River basin, plunge zones had undercut and slumping banks, minor streambed scouring near the base of the dam, and considerable gravel accumulation just downstream of the plunge pool (Csiki and Rhoads 2014).

Upstream movement of host-fish is a primary factor in mussel distribution, and recolonization of mussels can take many years. The colonization time following the Homer Park Dam failure in the middle of the 20th century suggests that recolonization of mussels can take decades, and is dependent upon available habitat and source populations of both mussels and host-fishes, as well as their life history strategies (Kappes and Haase 2012). Baker (1922) reported that the upstream distributions of 12 species were hindered by the presence of the Homer Park Dam; of those 12, only four have viable populations in the Vermilion River basin today (Stodola et al. 2013; INHS Mollusk Collection). Watters (1996) and Tiemann et al. (2007b) subsequently suggested that Mapleleaf and Pimpleback, both of which were included in Baker's 12 species, had dam-limited distributions due to the nature of their host-fishes. An examination of the INHS Mollusk Collections database revealed recent collections of a live Mapleleaf and a fresh-dead Pimpleback ~2.5 river kilometers upstream of the former dam in 2010, so we know that recolonization after dam removal occurs. Two other species, Pistolgrip and Mucket, are still extant near the former Homer Park

Dam but have lower population numbers in the Salt Fork (Stodola et al. 2013). Neither species has been found upstream of former impoundment. Mapleleaf, Pimpleback, and Pistolgrip utilize Channel Catfish (*Ictaluris punctatus*) and Flathead Catfish (*Pylodictis olivaris*) as hosts, whereas the Mucket uses a variety of fishes, including sunfishes and black basses (Watters et al. 2009). These fishes are common in the area and have somewhat large home ranges (INHS Fish Collection; Warren 2009; Tiemann et al. 2010). Prior to the passage of the *Clean Water Act*, the Salt Fork was heavily polluted with raw sewage and the freshwater mussel fauna was severely affected (Baker 1922; Van Cleave 1940; Matteson and Dexter 1966). It is possible that poor water quality may have prevented fish movement and subsequent mussel colonization of upstream reaches until recently. Today, the Salt Fork has several reaches with high mussel and fish diversity (Larimore and Bayley 1996; Tiemann 2008; Stodola et al. 2013).

Some freshwater mussels have experienced dramatic range reductions. When a basin contains multiple dams, as in the case in the Vermilion River, populations can become disjunct and fragmented partially due to dams restricting upstream movement of host-fishes, thus making recolonization difficult (Williams et al. 1993; Watters 1996; Cummings and Mayer 1997; Tiemann et al. 2007b). Two species, Yellow Sandshell and Black Sandshell, once occurred in both the Middle Fork and Salt Fork but are now found only downstream of the Danville Dam (INHS Mollusk Collection). These two species occur sporadically and often disjunctly throughout Illinois in medium to large rivers in firm sand and gravel substrates (Cummings and Mayer 1997; Tiemann et al. 2007a; Douglass and Stodola 2014; Stodola et al. 2014). Populations of the Black Sandshell, a state-threatened species, are increasing in several basins throughout its range (Douglass and Stodola 2014). Yellow Sandshell is thought to parasitize gars (*Lepisosteus* sp.), whereas Black Sandshell parasitize percids (e.g., *Sander* sp.) and centrarchids (*Lepomis* sp., *Micropterus* sp., and *Pomoxis* sp.) (Watters et al. 2009). Although the Danville Dam has a fish ladder present, its effectiveness of fish passage has not been tested or evaluated.

FUTURE CONSIDERATIONS

This study contributes insights into the effects of lowhead dams on freshwater mussel faunas in the Midwest, and suggests that they reduce mussel abundance and species richness immediately upstream and downstream from impoundments. These results are similar to those reported for fishes (Tiemann et al. 2004; Santucci et al. 2005; Slawski et al. 2008), mussels (Watters 1996; Dean et al. 2002; Tiemann et al. 2007b), and aquatic insects (Lessard and Hayes 2003; Tiemann et al. 2005; Maloney et al. 2008). Results from this project will help guide plans for the upcoming dam removal projects. Post-removal monitoring will allow for appropriate evaluation of changes in the mussel fauna following dam removal.

When making a decision to repair or remove a dam, it is important to consider that not all dams and dam removals have the same environmental consequences (Bednarek 2001; Sethi et al. 2004; Gangloff 2013). It is important to establish specific project objectives and examine all available data, despite the fact that some might be contradictory. Two of the dams (Ellsworth Park and Danville) in our study are scheduled for removal in the near future. Dam removal is viewed as a useful tool for stream restoration of altered habitat and reconnecting formerly isolated areas (Kanehl et al. 1997; Catalano et al. 2007; Maloney et al. 2008; Burroughs et al. 2009). With controlled demolition, dam removals can have little or no effect on downstream mussel fauna (Heise et al. 2013). Freshwater mussels would have an opportunity to naturally recolonize upstream regions of the Vermilion River basin if habitat conditions are optimal, host-fishes are extant, and source populations are in close proximity (Sietman et al. 2001; Tiemann et al. 2007b). Because these dams do not appear to be sediment traps (Csiki and Rhoads 2014), it seems unlikely that legacy sediments would smother mussels similar to those reported by Sethi et al. (2004). Another by-product of dam removal is stranding, desiccation, and predation of mussels within the former impounded area (Sethi et al. 2004). Given the geomorphology of the area, which includes differences in channel width and depth in relation to the dams (Csiki and Rhoads 2014), efforts could be made by natural resource agencies to return stranded mussels to the river to reduce mortality.

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River Research and Applications

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Low-head Dam Impacts on Habitat and the Functional Composition of Fish Communities

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ABSTRACT

The natural flow regime of many rivers in the United States has been impacted by anthropogenic structures. This loss of connectivity plays a role in shaping river ecosystems by altering physical habitat characteristics and shaping fish assemblages. Although the impacts of large dams on river systems are well documented, studies on the effects of low-head dams using a functional guild approach have been fewer. We assessed river habitat quality and fish community structure at twelve sites on two rivers; the study sites included two sites below each dam, two sites in the pool above each dam, and two sites upstream of the pool extent. Fish communities were sampled from 2012 to 2015 using a multi-gear approach in spring and fall seasons. We aggregated fishes into habitat and reproductive guilds in order to ascertain dams' effects on groups of fishes that respond similarly to environmental variation. We found that habitat quality was significantly poorer in the artificial pools created above the dams compared to all other sampling sites. Fast riffle specialist taxa were most abundant in high quality riffle habitats farthest from the dams while fast generalists and pelagophils were largely restricted to areas below the downstream-most impoundment. Overall, these dams play a substantial role in shaping habitat, which impacts fish community composition on a functional level. Utilizing this functional approach enables us to mechanistically link the effects of impoundments to the structure of fish communities and form generalizations that can be applied to other systems.

INTRODUCTION

River management has become focused on returning rivers to their natural flow regime, a dramatic shift from the era in which focus was on harnessing rivers' potential power and shaping them to human needs (Doyle *et al*., 2000). Ensuing from that era are over 85,000 dams in the United States (ASDSO, 2014) and fewer than 60 rivers in the contiguous United States with more than 100 kilometers free from impoundment (Doyle *et al*., 2000). This disruption of hydrologic connectivity can drastically alter ecological processes, influence flow regime, and change physical attributes of river systems (Ward *et al*., 2002; Pringle, 2003; Jansson *et al*., 2007). Key abiotic ecosystem components such as flow variability, channel size, substrate type and habitat diversity (distribution and quality of riffles, pools and runs) are largely determined by flow regime (Bunn and Arthington, 2002). Fragmentation and the resulting change in flow regime is a major driver of habitat structure in lotic systems (Bunn and Arthington, 2002). Typical habitat alterations triggered by dams include altered physicochemical parameters, a shift from lotic to lentic habitat upstream of the dam, and differences in sediment composition and distribution in the dams' vicinity (Bednarek, 2001; Butler and Wahl, 2010; Csiki and Rhoads, 2014). The lentic conditions upstream of dams facilitate the build-up of very fine sediments above the dam, filling in interstitial spaces in riverbed substrate (Bednarek, 2001). These pools also provide suitable conditions for disturbance-tolerant species to displace obligate riverine species and often favor the proliferation of exotic species (Bunn and Arthington, 2002; Guenther and Spacie, 2006; Slawski *et al*., 2008).

The impacts of large dams on migratory fishes and fish assemblages are well documented (Bunn and Arthington, 2002; Burroughs *et al*., 2010; Pess *et al*., 2008; Nislow *et al*., 2011). Studies on low-head dams are less common, but are becoming better represented in the literature (e.g. Cumming, 2004; Tiemann *et al*., 2004; Santucci *et al*., 2005; Chick *et al*., 2006; Poulet, 2007; Helms *et al*., 2011; Hastings *et al*., 2015). These studies collectively demonstrate the combined effects of dams as dispersal barriers and habitat manipulators that impact species richness and species abundances, restrict distributions and potentially isolate populations of river fishes. However, fewer studies have used environmental guilds to determine how low-head dams are affecting the functional structure of fish communities and to investigate the environmental factors driving these impacts (Poulet, 2007; Alexandre and Almeida, 2010; Musil *et al*., 2012). Functional assessments of communities provide a way to identify species with similar responses to environmental variation that can be used to form generalizations and predict community shifts (Welcomme *et al*., 2006; Noble *et al*., 2007). This trait-based approach to community ecology has been used in other ecological contexts. McGill *et al*., (2006) and Violle *et al*., (2007) demonstrated the advantage of functional traits in identifying general patterns in plant community ecology. These trait-based patterns offer predictive power and applicability across different systems. The current study applied this concept to aquatic systems by focusing on habitat and reproductive guilds as groups of fishes that respond to environmental variation in similar manners. Other studies using functional guilds (Poulet, 2007; Alexandre and Almeida, 2010; Musil *et al*., 2012) to evaluate impacts of low-head dams and weirs on fish communities did so in European river systems using generalized habitat and/or trophic guilds. We chose habitat and reproductive guilds to characterize dams' impact on fish assemblage structure in order to avoid the complications of ontogenetic diet shifts associated with assigning species to trophic guilds (Welcomme *et al*., 2006). The approach used in this study could be an effective way to determine how low-head dams affect fish communities and could be used to compare geographically and taxonomically different river systems. Furthermore, the authors are unaware of other studies in the American Midwest utilizing functional guilds to address the impacts of low-head dams on rivers.

To address the need for studies assessing low-head dam impacts using a functional approach, fish communities in a high quality but impounded Midwestern river system were sampled to: 1) determine the impact of low-head dams on the adjacent riverine habitat, 2) evaluate changes in fish composition across the system, and 3) relate these impoundments to the functional composition of local fish communities. The overall goal was to use functional traits of fishes to make generalizations about low-head dam impacts and to provide a predictive context for the impacts of dam removal.

METHODS

Study area

The impounded Vermilion and North Fork Vermilion Rivers are located in Danville, Illinois. The Danville Dam on the Vermilion River is an effective barrier between the lower 35 kilometers of Vermilion River mainstem and its 3,341 km^2 drainage area, including Illinois' only Designated Scenic River (IDNR, 2013). The Ellsworth Park Dam is located on the North Fork Vermilion River approximately 0.85 km upstream from the confluence of the Vermilion and North Fork Vermilion Rivers. Both dams are classified as low-head dams (structures under 4.6 meters in height as defined by USACE, 2013) and can be completely submerged when river discharges exceed bankfull which can occur multiple times every spring (Csiki and Rhoads, 2014; S. Smith, personal observation). Both structures have been deemed a public safety hazard and are slated for removal. A total of 12 sites 100 meters in length were monitored on the Vermilion River and the North Fork Vermilion River. Of the six sites located on each river, two were located below each dam (BD – below dam), two located in the pool above the dam (P – pool), and two river sites upriver of the pool extent (R – river; Fig. 1). Data were collected in fall and spring seasons from 2012 to 2015.

Habitat assessment

Modified Ohio Qualitative Habitat Evaluation Index (QHEI; Rankin, 2006) methods were used to determine macrohabitat quality scores for all reaches using the QHEI and Use Assessment Field Sheet. This index evaluates six principal metrics including substrate, instream cover, channel morphology, riparian zone, pool/glide and riffle-run quality, and gradient/drainage area. River width at each study site was measured using satellite imagery from 2013. Water quality parameters temperature (°C), dissolved oxygen (mg/L), pH and specific conductivity (µS/cm) were recorded at each site using a YSI Professional Plus (YSI Incorporated, Yellow Springs, OH) during all sampling periods. Surface water velocity was measured using a Hach Portable Velocity Meter (Hach Company, Loveland, CO) in mid-channel at each site.

Fish community sampling

Fish communities at each site were sampled using boat-mounted pulsed DC electrofishing (60 hertz, 25% duty cycle) with a 4000-watt generator and two Wisconsin droppers in 2014 and 2015. Fish communities sampled in 2012 and 2013 utilized either boat- or barge-mounted pulsed DC electrofishing methods as described in Hastings *et al.,* (2015). Including both boat and barge electrofishing data in the current study yields a holistic view of fish communities in the system. Data were collected in fall and spring seasons from 2012 to 2015. Sampling runs lasted for 30 minutes and included each bank and mid-channel. Supplemental sampling gear was season dependent: during fall sampling two bag seine pulls (4.6 m x 1.2 m, bag 1.2 m x 1.2 m x 1.2 m, 0.635 cm mesh) were conducted at each site and during spring sampling two mini-fyke nets (lead 4.5 m x 0.6 m, cab 3.0 m x 0.6 m x 1.2 m, 0.3 cm mesh) were set for 24 hours at each site. These gears sampled fish not susceptible to boat electrofishing even in high water conditions. All fish over 100 mm were measured for total length and weighed to the nearest gram; cyprinids and fish under 100 mm were euthanized and preserved in 95% ethanol for later identification. Individuals were identified to species. Species were assigned to habitat guilds using a modified version of guild classifications in Vadas and Orth (2000) and Persinger *et al*., (2011). The pool-run guild in the current study is unchanged from Vadas and Orth (2000) and Persinger *et al*., (2011). Following Persinger *et al*., (2011), the other three guilds in the current study (fast riffle, riffle-run and pool) are a combination of guilds described by Vadas and Orth (2000). These three guilds are equivalent to the riffle, fast generalist, and pool-cover guilds (respectively) described by Persinger *et al*., (2011); guilds were combined due to the similarity of habitats described by the guilds in Vadas and Orth (2000) and to match the available habitat in the system. Reproductive guild classifications were based on classifications described by Welcomme *et al*., (2006; after Balon (1975,1990)). Fish were assigned to guilds based on adult life history characteristics found in the literature or in Pflieger (1997).

Data analysis

Data were analyzed using R (version 3.2.1). For all analyses of QHEI, surface velocity, water quality parameters, species richness, Simpson's diversity, and index of biotic integrity (IBI) scores the individual sampling sites (Fig. 1) were pooled into below dam (BD), pool (P), and river (R) locations in each river to yield a total of six locations. This pooling allowed for a more robust view of the dams' impacts within each river. Differences in habitat quality as determined by QHEI scores were evaluated using analysis of variance (ANOVA) using year, river and location as fixed factors followed by Tukey's HSD post-hoc tests. Surface water velocity differences were evaluated using ANOVA as described above. Because of dramatically variable spring flows only data collected in fall sampling periods from 2012 to 2015 were used in velocity analyses. Differences in water quality parameters were evaluated using ANOVA with year, season, river and location as fixed factors followed by Tukey's HSD post-hoc tests. Species richness was determined by calculating the total number of species at each site and Simpson's index of diversity was calculated as $1/D$ where $D = \sum p_i^2$ (Simpson 1949), and index of biotic integrity scores were calculated following a revised IBI for Illinois streams (Smogor 2000). Species richness and Simpson's diversity measures were averaged over the entire sampling period to obtain a robust evaluation of these metrics in the system; differences were determined with ANOVA using river and location as fixed factors followed by Tukey's HSD post-hoc tests.

Index of biotic integrity scores were determined using ANOVA with year, season, river and location as fixed factors, but only years with complete fall and spring sampling (2013 and 2014) were used.

For compositional analyses, all fish data from all years and seasons were pooled in order to create a robust assessment of dam impacts on fish assemblages without the intra- and inter-annual variation that characterizes this system (Hastings *et al.*, 2015). Pooling and transforming these data into relative abundance data allow for analysis of the overall functional shifts generated by the dams as opposed to the analysis of temporal and environmental fluctuations, which is not the focus of this study. Furthermore, pooling data in this way eliminates the extreme variation in capture across the study, which further allows for focus on overall patterns. To analyze fish community data we used non-metric multidimensional scaling (NMS) based on Bray-Curtis similarity to assess patterns in relative abundances of taxa among individual sampling sites using the R package 'vegan'. Fish count data were transformed into relative abundance data for ordinations and follow-up univariate analyses in order to control for localized high densities of some taxa. Species that occurred only once or twice were deleted prior to analysis and dimensionality of ordinations was determined to minimize stress. Compositional analyses utilized fishes aggregated at the genus level while functional analyses used fish species grouped into habitat and reproductive guilds. The function *envfit* in the R package 'vegan' was used to assess impacts of environmental factors (such as QHEI metrics, water quality parameters and surface velocity) on genera composition among sampling locations. This function fits vectors representing environmental factors to NMS ordination plots and tests for statistical significance with 999 random permutation tests. Differences in habitat and reproductive guild relative abundance among locations over the whole sampling period were determined with ANOVA using river and location as fixed factors followed by Tukey's HSD post-hoc tests. Significant relationships between the proportional abundance of habitat and reproductive guilds and sampling locations were assessed using the *envfit* function in 'vegan' as above.

RESULTS

Physical river characteristics

Habitat quality (QHEI) differed among locations (ANOVA, $F_{4,24} = 16.38$, $P < 0.001$) but not among rivers (ANOVA, $F_{1,24} = 2.96$, $P = 0.098$) or years (ANOVA, $F_{3,24} = 2.12$, $P = 0.124$) with no significant interaction between terms. In both rivers, R locations had significantly higher habitat quality than P locations with the North Fork R location having the highest quality compared to all other locations (Tukey HSD, $P < 0.05$; Fig. 2). Surface velocity differed among years (ANOVA, $F_{2,18} = 10.95$, $P < 0.001$), between rivers (ANOVA, $F_{1,18} = 7.54$, $P < 0.05$) and among locations (ANOVA, $F_{4,18} = 11.37$, $P < 0.001$). No surface velocity data were available from 2012; therefore only data from 2013 to 2015 were used. Surface velocity was consistently higher below the Danville Dam in the Vermilion BD locations compared to P locations on both rivers (Tukey HSD, $P < 0.05$; Fig. 3). As might be expected, physicochemical parameters such as DO, temperature, pH and conductivity differed among seasons and/or years. Physicochemical parameters DO (ANOVA, $F_{3,103} = 87.53$, $P < 0.001$), temperature (ANOVA, $F_{3,112} = 38.95$, $P < 0.001$), pH (ANOVA, $F_{3,110} = 30.98$, $P < 0.001$), and conductivity (ANOVA, $F_{3,112} = 20.32$, $P < 0.001$) all differed among years. Temperature (ANOVA, $F_{1,112} = 109.33$, $P < 0.001$) and pH

(ANOVA, $F_{1,110} = 144.86$, $P < 0.001$) also differed between seasons. All parameters were within the ambient water quality standards set by the Illinois Environmental Protection Agency in all seasons and years except for low DO levels in fall 2012 (range of 3.38 mg/L – 5.37 mg/L; IEPA, 2004). Neither DO, temperature, pH nor conductivity consistently differed among locations. However, conductivity (ANOVA, $F_{1,112} = 97.31$, $P < 0.001$) and pH (ANOVA, $F_{1,110} = 4.47$, $P < 0.05$) were significantly higher in the Vermilion River compared to the North Fork Vermilion River.

Fish assemblages

A total of 24,247 fish were sampled from 2012 to 2015 representing 15 families, 40 genera, and 79 species. Total species richness ranged from 32 at NF_P2 to 59 at V_BD2 with a mean of 43.5 (Table 1). Vermilion BD had significantly more species compared to North Fork P, North Fork R, Vermilion P and Vermilion R locations (ANOVA, $F_{4,6} = 12.55$, $P < 0.05$). Simpson's diversity index reflected patterns in species richness with a wide range of values from 2.14 at NF_P2 to 14.51 at V_BD2 with a mean of 7.66 (Table 1). Simpson's diversity was significantly higher in Vermilion BD compared to North Fork P (ANOVA, $F_{4,6} = 3.14$, $P < 0.05$). The Vermilion River had significantly higher species richness (ANOVA, $F_{1,6} = 12.50$, $P < 0.05$) and a higher Simpson's diversity index (ANOVA, $F_{1,6} = 17.17$, $P < 0.01$) compared to the North Fork Vermilion River. Index of biotic integrity scores were calculated for each site and scores from 2013 and 2014 were averaged after determining that scores did not significantly differ by season or year (Table 1). The Vermilion River had significantly higher IBI scores compared to the North Fork (ANOVA, $F_{1,24} = 31.48$, $P < 0.001$) and IBI scores also differed by location (ANOVA, $F_{4,24} = 4.37$, $P < 0.01$). Vermilion BD had a higher average IBI compared to all North Fork locations and the Vermilion P and the Vermilion P and Vermilion R locations had higher IBI scores compared to the North Fork P (Tukey HSD, $P < 0.05$).

Fish community structure also showed strong responses to river identity and the presence of dams. Within the NMS ordination (Fig. 4; Table 2) there was a clear separation of rivers along the NMS1 axis, with the exception of NF_BD sites grouping with the Vermilion River sites that they are adjacent to. The genera *Etheostoma* and *Noturus* positively load on NMS2 axis near North Fork R sites while *Amia, Sander, Aplodinotus, Hybognathus,* and *Ammocrypta* are negatively loading on NMS1 with Vermilion BD and R sites (Fig. 4; Table 2). When environmental factors were overlaid on the genera NMS using *envfit*, surface velocity was a significant driver of composition along with river width and riparian zone width (*envfit*, $P < 0.05$).

Habitat guilds

Predictably, fish aggregated into habitat guilds reflected the habitat characteristics and overall habitat quality of the sampling sites. When overlaid on the genera NMS with *envfit*, habitat guild vectors separated out along both compositional axes, but more strongly along NMS1 (Fig. 4; Table 2). The riffle-run guild was strongly associated with Vermilion BD and R sites and the fast-generalist river fishes with NMS1 (*envfit*, $P < 0.005$). In contrast, pool-run habitat generalists associated with North Fork R and P sites (*envfit*, $P < 0.05$). Although not statistically significant, the fast-riffle guild composed of riffle specialist genera such as *Etheostoma* and *Noturus* was predominately associated with North Fork R sites.

When looking at differences in habitat guilds on a species level between rivers, there were more riffle-run species in the Vermilion River compared to the North Fork (ANOVA, $F_{1,6}$ = 20.12, P < 0.005, Fig. 5). In contrast, there were more habitat generalist pool-run species (ANOVA, $F_{1,6}$ = 27.94, P < 0.005, Fig. 5) and more riffle specialist species (ANOVA, $F_{1,6}$ = 25.48, P < 0.005, Fig. 5) in the North Fork Vermilion River compared to the Vermilion River. Furthermore, the relative abundance of riffle specialists differed by sampling location (ANOVA, $F_{4,6}$ = 16.09, P < 0.005, Fig. 5). Riffle specialist species were most abundant in the high quality North Fork R location compared to all other locations (Tukey HSD, P < 0.05). Although not statistically distinguishable, the high habitat quality North Fork R sites had the lowest abundance of pool species while the North Fork BD and P locations on both rivers had the greatest abundance.

Reproductive guilds

In contrast to habitat guilds associating with compositional axis NMS1, reproductive guilds associated with NMS2. Reproductive guilds strongly separated along NMS2 with guarder nest builders positively loading on that axis and non-guarder pelagophils and benthic spawners negatively loading (Fig. 4; Table 2). Comparing reproductive guilds by river revealed large differences that correspond well to composition (Fig. 4; Table 2). Guarder nest building species were significantly more abundant in the North Fork Vermilion River (ANOVA $F_{1,6}$ = 38.37, P < 0.001, Fig. 6) while non-guarder benthic spawners (ANOVA, $F_{1,6}$ = 35.18, P < 0.005, Fig. 6) and non-guarder pelagophils (ANOVA $F_{1,6}$ = 19.16, P < 0.005, Fig. 6) were more abundant in the Vermilion River. Pelagophil reproductive guild abundance (ANOVA, $F_{4,6}$ = 13.54, P < 0.005, Fig. 6) also differed by sampling location. Vermilion BD had significantly more pelagophils compared to all other locations (Tukey HSD, P < 0.05). Although not statistically distinguishable with Tukey HSD post-hoc tests, BD and R locations in the Vermilion River also had a higher abundance of non-guarder benthic spawners than the North Fork P and R locations. In contrast, North Fork P and R locations had a higher abundance of guarder nest builders than did Vermilion BD and R locations. River characteristics that were significant drivers of reproductive guild assemblages were river width and surface velocity (*envfit*, P < 0.05).

DISCUSSION

Dams affecting physical river characteristics

The linkage between habitat quality and surface water velocity with proximity to these impoundments are consistent with dam impacts noted in most systems (e.g. Kanehl *et al*., 1997; Santucci *et al*., 2005; Butler and Wahl, 2010). Poor habitat characterized by a deep pool, silty substrate, little to no surface velocity, and little habitat heterogeneity stretches approximately half a kilometer above the Ellsworth Park Dam and approximately 1.5 km above the Danville Dam. These pools consistently had the lowest surface water velocity while faster velocities were observed below both dams in the current study, a pattern also observed by Butler and Wahl (2010) in the Fox River, Illinois. These data suggest that the presence of these low-head dams strongly impacts both habitat quality and surface velocity in areas proximate to these structures. Similar to Alexandre and Almeida (2010), physicochemical parameters did not show significant relationships with location, suggesting that these low-head dams do not locally impact these abiotic factors. Additionally, a study by Csiki and Rhoads (2014) on the same dams as the current study determined that there were no discontinuities in river geomorphology upstream and downstream of these two dams; this is likely attributable to the dams' small size and run-of-river nature.

Fish assemblage structure

Species richness did not differ significantly between rivers; this result is not surprising when considering that each river has physical characteristics that favor different types of species and the small geographical scale of the study area. However, the Vermilion BD location had a higher number of species compared to P and R locations in both rivers which is likely a result of the accumulation of some species (mostly large bodied piscivores) observed below the Danville Dam. Since the Danville Dam is the first barrier on the Vermilion River to fish moving upstream from the unimpounded Wabash River and is impassable except when river discharge is high, many riverine fishes are restricted to the area below the dam and were not observed in the river above the dam (i.e. *Lepisosteus, Amia* and *Sander*). Santucci *et al*., (2005) found similar results in the Fox River (Illinois) where riverine fish distributions were largely restricted to river sections below the downstream-most impoundment. A similar study by Poulet (2007) on European rivers also found higher total species richness below weirs compared to reference sites (sites free from weir influence). Furthermore, habitat immediately upstream of the Danville Dam is more lentic than lotic in character and riverine fishes would likely prefer the fast flowing waters below the dam.

The distribution of flow-dependent fishes likely drives the separation between rivers in the NMS plot, along with the higher abundance of *Percina* and *Etheostoma* darters in the North Fork compared to the Vermilion. The North Fork is a smaller tributary of the Vermilion with a stretch of high quality riffle habitat suitable for intolerant fish taxa that is located approximately half a kilometer upstream of the Ellsworth Park Dam. Similar to our findings, Santucci *et al*., (2005) also noted that darter species were typically absent from the middle of a river reach impounded by multiple low-head dams. The notable clustering of North Fork BD sites with Vermilion sites in the NMS plot validates our field observations that the pooling effect seen directly upstream of the Danville Dam may extend into NF_BD1 (at the confluence of the two rivers). Surface velocity in this BD site was often very low, and habitat characteristics strongly resemble those in the Vermilion P sites. This suggests that local habitat and therefore fish community composition can be influenced by both upstream and downstream factors in our study area and exemplifies the extent of dams' compounding impacts on impounded river systems.

Habitat and reproductive guild structure

The functional guild concept has been adopted by many to describe fish community structure in river ecosystems (Poff and Allan, 1995; Poulet, 2007; Alexandre and Almeida, 2010; Musil *et al*., 2012). This concept states that fish assemblages are determined by the functional diversity of a local system in terms of available habitat and hydrologic processes. Given the well-documented effects of impoundments on altering the physical attributes of rivers (Ward and Stanford, 1995; Bunn and Arthington, 2002; Jansson *et al*., 2007) we would expect a concomitant change in fish functional composition. Overall, the current study supports others that have shown that fish habitat guilds reflect the habitat characteristics and quality of the local environment (Poulet, 2007; Alexandre and Almeida, 2010; Musil *et al*., 2012) and further finds that the habitat changes resulting from the low-head dams on these rivers play a role in structuring both habitat and reproductive functional groups. Additionally, this study found the two functional guilds were related directly to different compositional axes within the NMS, suggesting that the functional approaches applied here reflect different, independent, functional dimensions of fish communities. The larger component of fish community composition, NMS1, was related to habitat guilds. In contrast, reproductive guilds largely varied along NMS2 and were associated with river width and surface velocity in our system. These patterns strongly argue for the utility of a functional approach in mechanistically understanding dam impacts on fish communities. Documenting dams' effect on trait-based groups of fishes allows for the comparison of river systems influenced by low-head dams and contributes to the utility of predicting how fish communities might be impacted by low-head dams and their removal.

Clear patterns in habitat guilds emerged relative to the location of the dams in both rivers. The presence of the Danville Dam likely prevents upstream passage of large bodied fishes into the North Fork during most of the year. Similar to Musil *et al*., (2012), the current study finds that rheophilic fishes show a very strong response to the presence of impoundments. One of the most notable patterns was the difference in fast riffle specialist taxa abundance between the North Fork R location and every other location in the study area. High quality riffles and habitat heterogeneity in rivers and streams (here, the North Fork R location) strongly cater to demersal, sensitive taxa such as darters and madtoms (Vadas and Orth, 2001) as illustrated in the current study by the distribution of *Etheostoma* and *Noturus.* Additionally, there were very few pool genera in this high quality habitat. The apparent patterns in habitat guilds coupled with the discrepancy in surface velocity among BD, P and R locations is consistent with Vadas and Orth's (2001) research defining the importance of surface velocity in structuring habitat guilds.

It is clear that the poor habitat created above both of these low-head dams impacts fish assemblages. Although these structures are likely intermittently submerged when river discharge is high during spring months, the lack of large predators such as *Lepisosteus, Amia,* and *Sander* in any habitat above the Danville Dam suggests that either the opportunities for dam passage are few during the year, and/or the poor habitat and lack of surface velocity in the pool above the dam is itself a deterrent to movement.

Fish aggregated into reproductive guilds also showed differences in abundance between locations. Although not statistically significant, the highest relative abundance of benthic spawners was found in Vermilion BD and R locations and highest relative abundance of nest builders found in North Fork P and R. These abundances were associated with river width and surface velocity, likely reflecting overall habitat quality for nest building or substrate for spawning. Pelagophils were almost entirely sampled in the Vermilion BD sites where surface velocity is strong throughout the year and there are no impoundments downstream to hinder egg dispersal; Perkin *et al*., (2015) also found decreased abundances of pelagophils in the presence of anthropogenic barriers.

A principal factor that overlays the effects of impoundments is river size and discharge. Habitat guilds differed between the two rivers; fast generalist riffle-run genera were more abundant in the larger Vermilion River while eurytopic pool-run genera were more abundant in the North Fork Vermilion River. Reproductive guild assemblages differed between rivers as well, with benthic spawners more abundant in the larger Vermilion River and nest builders more abundant in the North Fork Vermilion River. Although river size has a critical role in shaping assemblages, distinct patterns in both habitat and reproductive guilds within each river suggest that the dams are also an important driver of community structure.

Implications

Both of the low-head dams in the current study are scheduled for removal, and data from multiple years and seasons prior to dam removal is essential to predict how removal will impact this system. Data presented here suggest that certain taxa are more susceptible to impoundments than others, notably, fast riffle specialists such as darters that are restricted in their dispersal and sensitive to poor habitat. In these rivers, this may have important implications for the Illinois state endangered Bluebreast Darter (*Etheostoma camurum*) that was only sampled downstream of the Ellsworth Park Dam during this study. This impoundment appears to be restricting dispersal of this darter and impeding access to the high quality habitat available upriver.

This study furthers our understanding of how low-head dams shape habitat and illustrates the myriad impacts of physical habitat on fish assemblage structure. Notably, this study also contributes to the growing body of literature using functional guilds as a way to effectively assess environmental impacts. Based on our findings, we advocate for the viability of functional guilds in understanding dam impacts on Midwestern rivers. Our research illustrates that functional analyses of fish assemblages are valuable in mechanistically linking the effects of impoundments to the structure of fish communities as well as forming generalizations that can be applied to other systems.

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Table 1. Measurements of species diversity and biotic integrity for all study sites. Species richness and diversity index scores calculated from data spanning 2012 to 2015; IBI scores calculated from data collected in 2013 and 2014.

Site Name	Species Richness	Simpson's Diversity	Mean IBI Score	IBI Integrity Class	River Name
V_BD1	57	9.71	46.5	Good	Vermilion
V_BD2	59	14.51	47.0	Good	Vermilion
V_P1	35	8.11	31.8	Fair	Vermilion
V_P2	44	11.36	42.3	Fair	Vermilion
V_R1	45	7.13	41.8	Fair	Vermilion
V_R2	41	11.18	39.0	Fair	Vermilion
NF_BD1	44	8.11	29.3	Poor	North Fork Vermilion
NF_BD2	47	10.16	40.8	Fair	North Fork Vermilion
NF_P1	35	2.54	24.8	Poor	North Fork Vermilion
NF_P2	32	2.14	27.5	Poor	North Fork Vermilion
NF_R1	40	2.32	30.5	Fair	North Fork Vermilion
NF_R2	43	4.67	33.3	Fair	North Fork Vermilion

Table 2. Abbreviations of scientific genera names described in Figure 4.

Abbreviation	Full Genus Name	Abbreviation	Full Genus Name
Ambl	*Ambloplites*	Hype	*Hypentelium*
Amei	*Ameiurus*	Hypo	*Hypophthalmichthys*
Amia	*Amia*	Icta	*Ictalurus*
Ammo	*Ammocrypta*	Icti	*Ictiobus*
Aplo	*Aplodinotus*	Labi	*Labidesthes*
Camp	*Campostoma*	Lepi	*Lepisosteus*
Carp	*Carpiodes*	Lepo	*Lepomis*
Cato	*Catostomus*	Micr	*Micropterus*
Cten	*Ctenopharyngodon*	Miny	*Minytrema*
Cypr	*Cyprinus*	Moro	*Morone*
Doro	*Dorosoma*	Moxo	*Moxostoma*
Eric	*Ericymba*	Notr	*Notropis*
Erim	*Erimyzon*	Notu	*Noturus*
Esox	*Esox*	Perc	*Percina*
Ethe	*Etheostoma*	Phen	*Phenacobius*
Fund	*Fundulus*	Pime	*Pimephales*
Gamb	*Gambusia*	Pomo	*Pomoxis*
Hybog	*Hybognathus*	Pylo	*Pylodictis*
Hybop	*Hybopsis*	Sand	*Sander*

Figure Legend

Figure 1. Map of Vermilion River and North Fork Vermilion River sampling sites in Danville, Illinois. Sites include below dam sites (BD1, BD2), pool sites (P1, P2) and river sites (R1, R2). Danville Dam located between V_BD2 and V_P1, Ellsworth Park Dam located between NF_BD2 and NF_P1.

Figure 2. Qualitative Habitat Evaluation Index (QHEI) scores from all sampling sites. Vermilion River is symbolized by the filled triangles and the North Fork Vermilion River represented by the open triangles. Below dam sites – BD; pool – P; and river – R.

Figure 3. Surface water velocity (flow) rates (m s⁻¹) from all study sites on each river. Vermilion River – V_; North Fork Vermilion River – NF_; below dam – BD; pool – P; river – R.

Figure 4. NMS ordination plots showing the twelve study sites on each river (a), genera (b), habitat guilds (c), and reproductive guilds (d). In (a) sites on the Vermilion River are symbolized by the open symbols and the North Fork sites represented by the filled symbols. Below dam sites – BD; pool – P; and river – R. Genera in (b) are abbreviated by the first four or five letters of the scientific genus name. Plots (c) and (d) are vectors plotted by <i>envfit</i> and overlaid on the site and genera plots; length and directionality of vectors correspond to the strength of correlation with sites and genera. Refer to Table 2 for a list of genera corresponding to the abbreviations in (b).

Figure 5. Relative abundances of fish aggregated into habitat guilds at each river location.

Figure 6. Relative abundances of fish aggregated into reproductive guilds at each river location.

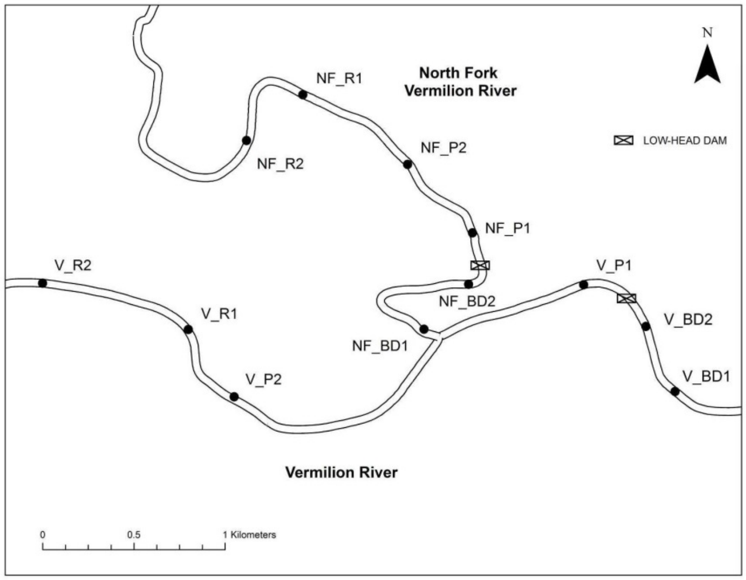

Figure 1. Map of Vermilion River and North Fork Vermilion River sampling sites in Danville, Illinois. Sites include below dam sites (BD1, BD2), pool sites (P1, P2) and river sites (R1, R2). Danville Dam located between V_BD2 and V_P1, Ellsworth Park Dam located between NF_BD2 and NF_P1.
Fig. 1
215x166mm (300 x 300 DPI)

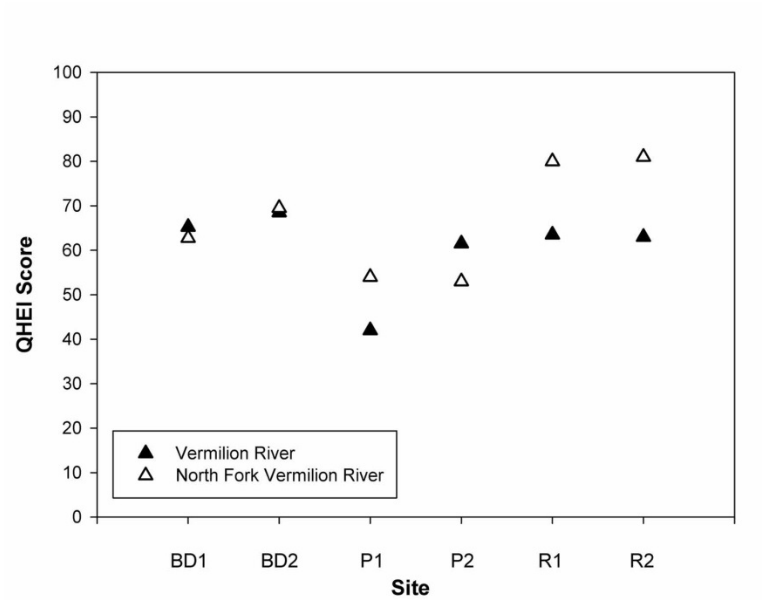

Figure 2. Qualitative Habitat Evaluation Index (QHEI) scores from all sampling sites. Vermilion River is symbolized by the filled triangles and the North Fork Vermilion River represented by the open triangles. Below dam sites – BD; pool – P; and river – R.
Fig. 2
119x94mm (300 x 300 DPI)

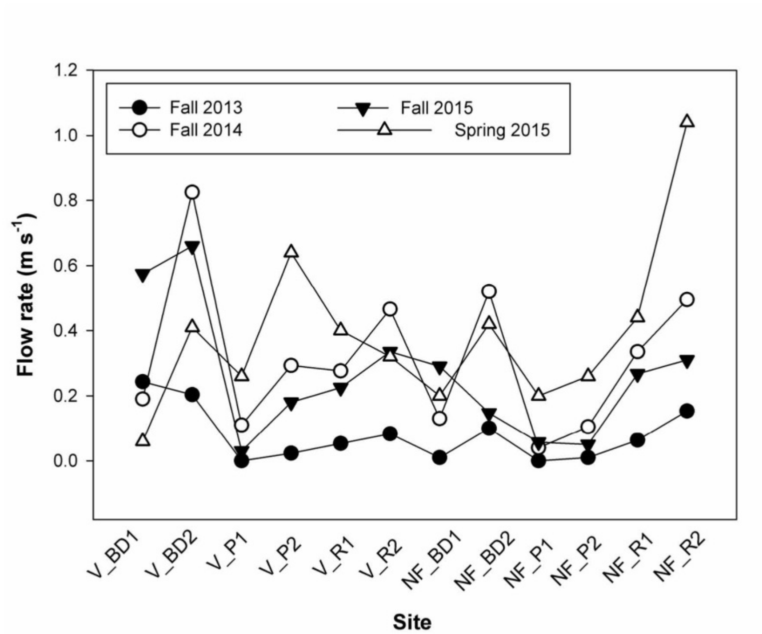

Figure 3. Surface water velocity (flow) rates (m s^{-1}) from all study sites on each river. Vermilion River – V_; North Fork Vermilion River – NF_; below dam – BD; pool – P; river – R.
Fig. 3
124x103mm (300 x 300 DPI)

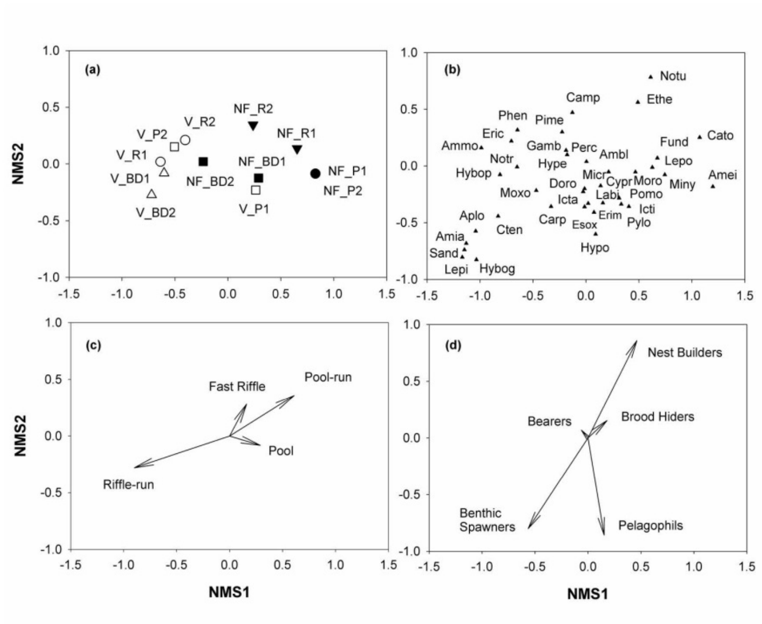

Figure 4. NMS ordination plots showing the twelve study sites on each river (a), genera (b), habitat guilds (c), and reproductive guilds (d). In (a) sites on the Vermilion River are symbolized by the open symbols and the North Fork sites represented by the filled symbols. Below dam sites – BD; pool – P; and river – R. Genera in (b) are abbreviated by the first four or five letters of the scientific genus name. Plots (c) and (d) are vectors plotted by *envfit* and overlaid on the site and genera plots; length and directionality of vectors correspond to the strength of correlation with sites and genera. Refer to Table 2 for a list of genera corresponding to the abbreviations in (b).

Fig. 4

176x145mm (300 x 300 DPI)

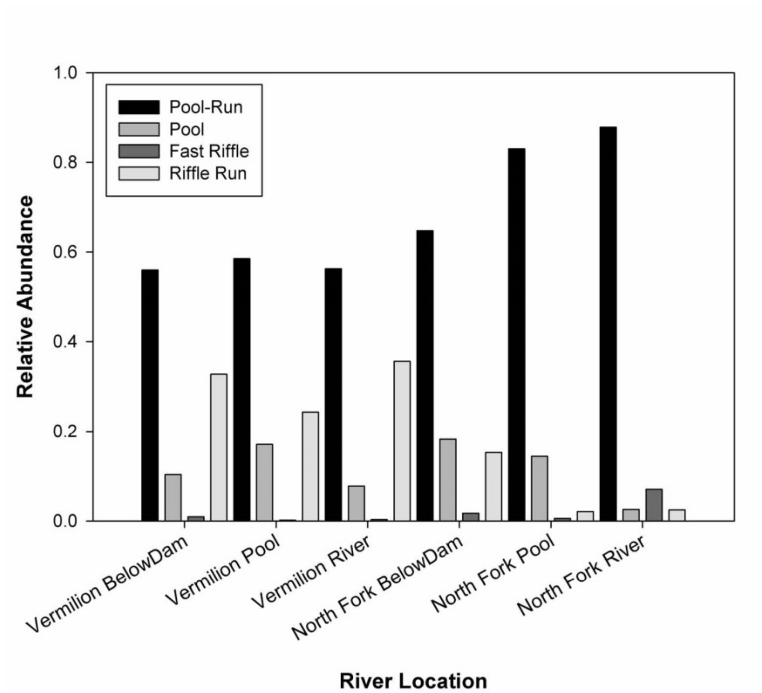

Figure 5. Relative abundances of fish aggregated into habitat guilds at each river location.
Fig. 5
137x124mm (300 x 300 DPI)

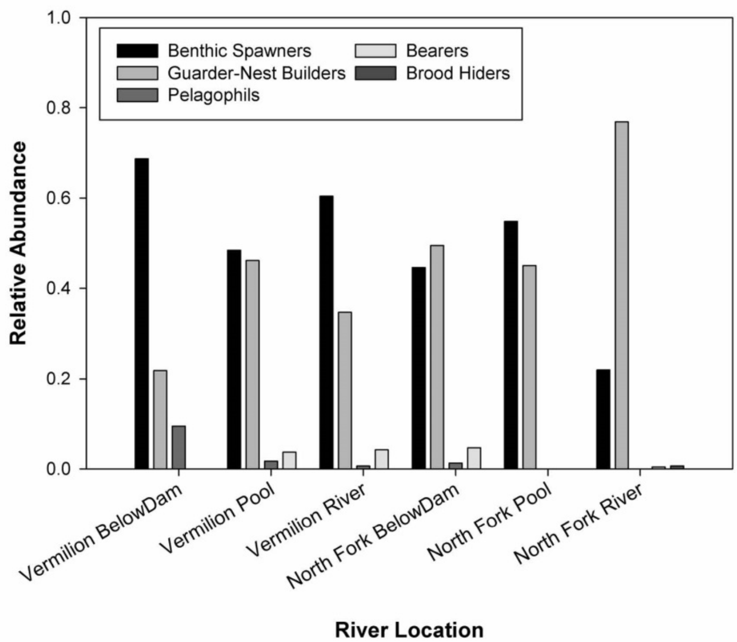

Figure 6. Relative abundances of fish aggregated into reproductive guilds at each river location.
Fig. 6
136x123mm (300 x 300 DPI)