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Low-Head Dam Removal Increases Functional Diversity of Stream Fish Assemblages

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LOW-HEAD DAM REMOVAL INCREASES FUNCTIONAL DIVERSITY OF STREAM FISH ASSEMBLAGES

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ABSTRACT

Despite the growing number of dam removals to date, very few have been studied to understand their impacts on stream fish communities. Despite being the most common type of dam in the U.S., an even smaller proportion of studies focus on the impacts of low-head dam removals, instead, focusing on the impacts of removal of larger dams. In this study, two previously impounded Illinois rivers were monitored to assess the impacts of low-head dam removal on the functional assemblage of stream fishes. This was accomplished by aggregating fishes into habitat and reproductive guilds, relating community changes to habitat, environmental metrics, and stream quality. Prior to removal, the slackwater guild was the most prevalent habitat guild throughout both rivers, while nest builders and benthic spawners were the most abundant reproductive guilds. Following removal, habitat conditions and fish assemblages improved throughout both rivers, with improvements in QHEI, IBI, water temperature, and dissolved oxygen, as well as a shift to more evenly distributed representation of both guild types. The improvements in environmental metrics and overall stream quality, particularly in the impounded habitats, indicate diminished habitat homogeneity, and a shift towards natural habitat diversity. This habitat diversification likely led to the restoration of a range of potential niches, thereby increasing the array of guild types that may inhabit these rivers, while simultaneously limiting single-guild dominance.

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INTRODUCTION

To date, more than 1,400 dams have been removed from U.S. waterways (American Rivers 2019), however, less than 10% of these removals have been studied to understand their impacts on stream fishes (Bellmore *et al.* 2017). Fishes inhabiting impounded streams are particularly vulnerable to dams and the resulting ecological impairments (Oliveira *et al.* 2018; Turgeon *et al.* 2019; Barbarossa *et al.* 2020). Other studies have exemplified this susceptibility in fishes, documenting the increase in homogenization of assemblages in impounded streams with the higher spring flow (Hastings *et al.* 2016). The cause of this susceptibility could be due to several dam induced impairments, including fragmentation of populations, altered hydrology and flow regime, reduced lateral exchange of sediments and nutrients, and alteration of biological and physical characteristics of the river channel and flood plain (Bednarek 2001). Of these impairments, the shift from lotic to lentic conditions is particularly problematic to many stream fishes. Such a shift often results in only fishes adapted to lentic conditions and those possessing a high degree of functional plasticity able to persist, as they are capable of inhabiting lacustrine conditions (Agostinho *et al.* 2008; Turgeon *et al.* 2019). Such plasticity and tolerance is not common in fishes, contributing to the reduced diversity and abundance often associated with impounded systems (Agostinho *et al.* 2008; Turgeon *et al.* 2019).

Although the call for many dam removals is often due to dam age and degradation that diminish utility (Doyle *et al.* 2003), increased public awareness of the ecological costs imposed by dams and the intent to restore the system to a more natural state are also a driving force for removal (Bednarek 2001; Poulos *et al.* 2014; Poulos & Chernoff 2016). Despite the intent to restore the system, a successful outcome is uncertain (e.g., Cheng & Granata 2007; Stanley *et al.* 2007; Chang *et al.* 2016). Following dam removal, a variety of habitat alterations may occur; for example, unobstructed flow would allow accumulated sediments to move downstream, resulting in altered channel morphology, habitat conditions, and nutrient transport (Hart *et al.* 2002), potentially degrading downstream conditions. Removing impoundments may also reestablish natural flow regimes and facilitate movement of migratory fauna, resulting in genetic or compositional changes (Hart *et al.* 2002; Catalano *et al.* 2007; Haponski *et al.* 2007; Ding *et al.* 2019). Limited research examining such ecological shifts as a result of dam removal and the impacts on stream fishes causes uncertainty in whether dam removal will be a beneficial or detrimental course of action.

In assessing the relationship between dams and stream fishes, priority has been given to larger dams at least 15 m high or that impound 3 million m^3 of water (ICOD 2011). Despite being the majority of dams in the U.S. (USACE NID 2018; Iowa Department of Natural Resources 2021), little research has focused on low-head dams (no higher than 9 m). Within the limited studies on low-head dams, even fewer analyze the impacts of removal and the responses of stream fish communities (Bellmore *et al.* 2017). Rather, these studies largely focus on understanding the effects imposed on stream fishes and the environment in response to the presence of dams (Butler & Wahl 2010; Alexandre & Alemida 2010; Smith *et al.* 2017). Due to this, there is a necessity to increase our understanding of low-head dam removal, especially with the increasing rate of removals (Poff & Hart 2002).

Although a few studies document low-head dam removal and their effects on fishes, an even smaller proportion analyze functional impacts on stream fish communities by examining guilds (Catalano *et al.* 2007; Dorobek *et al.* 2015; Ding *et al.* 2019). Guilds were created to be fish indicators that respond to variations in a rivers' hydrology, geomorphology, and habitat structure (Welcomme *et al.* 2006). Because many of the factors used to aggregate fishes into guilds may be impacted by dam presence and removal, documenting changes in guild structure should provide functional understanding. This approach is especially useful as it emphasizes connections between changes in community composition and environmental parameters such as increased abundance of pelagophils in response to improved connectivity or increased abundance of riffle and run species in response to increased lotic habitat.

Linking environmental drivers to community composition provides a benchmark to determine the course of action necessary to improve the system. While a guild system allows for this assessment, understanding of relationships between the environment and community may be strengthened by the simultaneous use of additional statistical techniques. The index of biotic integrity (IBI; Karr 1981) is one such approach. IBI computes an index of stream quality by integrating various aspects of fish communities (i.e. proportion of reproductive and feeding groups), as well as observed environmental conditions, and comparing them to expected conditions of a similar, undisturbed river or stream (Karr 1981; Oberdorff & Hughes 1992). Because several attributes analyzed by IBI are synonymous with those examined in a guild structure, utilizing the techniques in conjunction will emphasize trends in functional composition in response to potential environmental shifts following dam removal.

Given the paucity of functional assessments of dam removals, I analyzed guild changes in stream fish communities in response to low-head dam removal. Specifically, I delineated fishes into habitat and reproductive guilds, to assess functional changes in community composition. To do this, I sampled two streams in Illinois which had low-head dams removed. Fishes and habitat data were collected both pre- and post-removal to; (i) document immediate habitat responses to low-head dam removal (ii) document functional changes in stream fishes in response to low-head dam removal and (iii) provide detailed information on environmental and stream fish responses. I predicted that overall health of the rivers would improve, and that flow rate and dissolved oxygen would improve among all habitat types in response to dam removal, but the greatest improvements would occur in the impounded reaches. I also hypothesized that dominance of lacustrine-adapted fishes would dissipate, and functional group diversity would increase within these rivers.

METHODS

Study Site

This study analyzed two tributaries of the Wabash River located near Danville, Illinois: The Vermilion River and the North Fork Vermilion River (Figure 1). Both rivers were impounded by low-head dams since the early 1900s, the Danville Dam and Ellsworth Park Dam respectively, until they were removed in 2018 (IDNR 2018). The Danville Dam was the furthest downstream impoundment on the Vermilion River, located between the lower 35 km of the river and the remaining 3,341 km^2 upstream drainage area. Whereas the Ellsworth Park Dam was located on the North Fork Vermilion River, about 4 km downstream of Lake Vermilion, and just upstream of the confluence of the two rivers (IDNR 2018). Sampling took place in six study sites within each river. Each site measured 100 m in length and consisted of three habitat types: two downstream of the dam (DWN), two within impounded areas (IMP) and two within the runs of the rivers (ROR) (Figure 1; Hastings *et al.* 2015). Pre-removal collection occurred in the fall of 2012-2015 and post removal collection occurred in the fall of 2018-2020, except in the North Fork Vermilion River where sampling did not occur in 2018 as the timing of the dam removal conflicted with sampling events.

Fish Sampling

I collected fishes using DC electrofishing methods as described in Hastings *et al.* (2015); by boat on the Vermilion River and by barge on the North Fork Vermilion River where waters levels were too shallow waters for boat navigation. Sampling occurred at 30-minute intervals at each site and fish were identified to species, weighed (g) and measured (total length, mm) after each effort. However, any specimen with a total length below 100 mm was not weighed, and those that were not easily identified in the field (i.e. *Cyprinella*) were euthanized and preserved in 95% ethanol to be identified in the lab. Two species of redhorse inhabiting these rivers, the Black Redhorse and Golden Redhorse (*Moxostoma duquesni* and *Moxostoma erythrurum*, respectively) are not easily distinguished. Because of this similarity, when these species were collected, they were photographed and released. The photographs were examined in the lab, where lateral line scales were counted to determine species (Golden Redhorse = 39-43 scales and Black Redhorse=44-47 scales).

Assessment of Stream Health

Stream health was evaluated by analyzing abiotic factors using Ohio Qualitative Habitat Evaluation Index scores (QHEI; Rankin 2006) and by analyzing biotic factors, using Index of Biotic Integrity scores for each site (IBI; Karr 1981; Smogor 2000). Six variables are utilized to compute QHEI: substrate, instream cover, channel morphology, riparian zone and bank erosion, pool/glide and riffle/run quality, and gradient, designating a score to each. Scores are then summed to compute an overall score. IBI is calculated using ten biotic metrics, including number of native fish species, number of intolerant species, proportion of tolerant species, and the proportions of several reproductive and feeding groups. Each metric is then adjusted based on wetted stream width and, similarly to QHEI, summed to compute an overall score (Smogor 2000).

Water quality metrics were also taken every sampling event from the thalweg of each site, with a YSI Professional Plus (YSI Incorporated, Yellow Springs, OH). The YSI meter recorded water temperature (C°), specific conductivity (µS/cm), dissolved oxygen (mg/L), and pH. Other metrics assessed include surface water velocity (m/s), taken from the middle of the channel using a Hach Portable Velocity Meter (Hach Company, Loveland, CO), turbidity (m) by use of a secchi board, and stream width (m).

Guild Assignment

Habitat guilds were constructed following Spurgeon *et al.* (2019) from a stream in Nebraska. In their study, five habitat guilds were formulated; lobate margin, run, riffle, slackwater and habitat generalist. The lobate margin guild was described as including fishes that inhabit areas of low velocity and shallow depths on channel margins. The run guild includes fishes that are most often found in the main channel, where depths and velocities tend to be greater. The riffle guild was characterized by fishes found in clearer waters, with slightly lower velocities than main channels and containing coarse substrate. Fishes belonging to the slackwater guild are those preferring off channel pools or backwaters near stream edges. Finally, habitat generalist fishes are those that are not associated with a specific habitat type and are found in several types of habitats (*Spurgeon et al*. 2019). Fishes collected in our study not listed by Spurgeon *et al.*, were placed into guilds based on habitat preferences found in literature (Pflieger 1997; Page & Burr 2011).

Reproductive guilds were constructed following Simon (1999), which is a modified classification based on Balon (1975, 1981). The reproductive guilds used here include:

pelagophils, benthic spawners, brood hiders, nest builders, and live bearers. However, only one species of live bearer, the Mosquitofish (*Gambusia affinis*), occurred in our study, and was only collected in the North Fork Vermilion prior to dam removal. The reproductive guilds used were modified to group several different guilds into more generalized ones following Smith *et al.* (2017). For instance, in this study, nest builders include most species listed as 'guarders' by Balon (1981) and Simon (1999), whereas species listed as 'nonguarders' by Balon (1981) and Simon (1999) are partitioned into either pelagophils, brood hiders, or benthic spawners.

Data Analysis

Data used for each analysis consisted of catch per unit effort (CPUE) using species abundance aggregated into habitat and reproductive guilds. The resulting CPUE values were log10 + 1 transformed to down-weight abundant taxa. All environmental data, water temperature, dissolved oxygen, QHEI and IBI were log transformed, except for flow, which was log + 1 transformed in order to combat the zeros in the data set. Environmental data were transformed to improve normality as well as to increase clarity of potential trends. Following these transformations, an array of two-way analysis of variance (ANOVA's) were used to determine impacts of dam removal that may explain trends in functional composition, QHEI, IBI, environmental variables and overall species abundances. Additionally, to control for any variation that may occur between the two systems, river was included into the analyses as a blocking variable.

Trends in functional composition associated with dam removal were examined using nonmetric multidimensional scaling (NMDS) ordinations using Bray-Curtis dissimilarity. The guild/site matrices used to compose the NMDS consisted of the log + 1 transformed CPUE grouped by guild type (habitat or reproductive). The relationships of guild and overall stream health (QHEI and IBI) were related to the ordinations by plotting a series of vectors. Significance of functional responses to habitat and dam removal were assessed by a permutational multivariate analysis of variance (PERMANOVA) separately for habitat and reproductive guilds, again including river as a blocking factor. PERMANOVAs utilized Bray-Curtis dissimilarity, consisted of 10,000 permutations and were conducted with the *adonis* command in the "-*vegan*-" package of R.

To assess the impacts of dam removal on guild assemblage, the Shannon-Weiner diversity index (Shannon and Weaver, 1949), and abundance of each functional group were analyzed. Diversity was calculated using the same log + 1 transformed data described in the NMDS ordination above and CPUE of each functional group was calculated. Two-way analyses of variance (ANOVA's) using the same structure as described in the PERMANOVA and ANOVA's above were then used to analyze these variables. Live bearers were omitted from the abundance analysis because of low occurrence in the dataset. R version 3.6 (R Foundation for Statistical Computing) were used for all analyses.

RESULTS

Stream Health

Water temperature and dissolved oxygen level were significantly impacted by dam removal (Table 1), with water temperatures decreasing and dissolved oxygen increasing following removal (Figure 2). However, neither differed among rivers or locations. Flow was significantly higher in the Vermilion River as well as in the downriver and run of river habitats (Figure 2) but showed no change in response to dam removal (Table 1).

Neither QHEI nor IBI differed between rivers, but both varied significantly among locations (Table 1; Figure 3), with both QHEI and IBI highest in the run of river habitats, and lowest in the impounded habitats. IBI also increased significantly following dam removal (Table 1). QHEI overall increased following dam removal but the changes were largest in impounded reaches, resulting in a significant location × removal interaction (Figure 3). Similarly, IBI increased following dam removal in all sites, but impounded regions experienced greater improvements the other habitats (Figure 4).

Overall Abundances

Following dam removal, abundances of fishes increased throughout both rivers. (ANOVA $F_{1,71} = 15.27$, $P = 0.0002$; Figure 5). Abundance of fishes also responded to location (ANOVA $F_{2,71} = 5.29$, $P = 0.0072$) and differed between rivers (ANOVA $F_{1,71} = 11.24$, $P = 0.0013$). Abundance increased in all sites but experienced the greatest increase in the impounded reaches, despite no detection of a location by removal interaction (ANOVA $F_{2,71} = 1.74$, $P = 0.1821$; Figure 5). Abundances were overall higher in the North Fork Vermilion (all habitats, pre and post removal; Figure 5).

Functional Assemblages and Guild Diversity

There was a clear impact of dam removal on habitat guild composition in both the Vermilion and North Fork Vermilion Rivers (Figure 6; Table 2). PERMANOVA results supported guild compositional differences between rivers and among locations as would be expected. Dam removal also significantly altered habitat guild composition, but this was consistent across habitats, resulting in a non-significant removal × location interaction. These changes can be visualized in the NMDS ordination. Slackwater and lobate margin guilds positively loaded on the NMDS2 axis, and negatively on NMDS1. Riffle, run and habitat generalist guilds were negatively loaded on both axes. In both rivers dam removal resulted in a marked negative shift on NMDS1. Habitat guild composition also became less heterogeneous across sites following dam removal (Figure 6). In particular, pre-removal habitat guild compositional heterogeneity was lowest in impounded habitats.

Reproductive guild composition within both rivers were also clearly impacted by dam removal (Figure 6; Table 2). As with habitat guilds, reproductive guild composition differed between rivers, among habitats, and with dam removal. Again, there was no interaction between location and dam removal, indicating system-wide compositional changes. These compositional changes can be visualized in the NMDS ordination on reproductive guild composition. Live bearers, nest builders and to a lesser extent brood hiders were positively loaded on NMDS2 and negatively loaded on NMDS1. Benthic spawners and pelagophils were negatively loaded on both NMDS1 and NMDS2 (Figure 6). Dam removal resulted in a general negative shift along NMDS1 (Figure 6). Reproductive guild composition became more homogenous across all habitats, following dam removal (Figure 6). Additionally, benthic spawners and brood hiders were the strongest influencers of abundance redistribution, with pelagophils also influencing the shift to a lesser degree (Figure 6).

QHEI and IBI were strongly related to the observed changes in functional composition. QHEI was most strongly associated with riffle specialists and to a lesser extent the run habitat guilds (Figure 6). In the ordination of reproductive guilds, QHEI was strongly related to the abundance of benthic spawners and effectively independent from nest builders and live bearers (Figure 6). Guilds associated with QHEI were similarly associated with IBI, however these relationships were stronger (Figure 6). Within reproductive guilds, both metrics were nearly identical in their guild relationships. Both metrics reflected the compositional changes associated with dam removal, regardless of guild type.

Diversity of both guild types increased following dam removal by location (Table 3; Figure 7). Dam removal also significantly varied by location in both guild types (Table 3; Figure 7). However, only habitat guild diversity differed between rivers, with higher diversity in the North Fork Vermilion (Table 3; Figure 7). While increases in the diversity of both guild types was greatest within impounded reaches, a significant location by removal interaction only occurred in reproductive guild diversity (Table 3).

Responses of Individual Guilds

All habitat guilds responded to location (Table 4; Figure 8) and all guilds, except the run guild, differed between rivers (Table 4; Figure 8). Dam removal increased the abundance of all habitat guilds, except for the slackwater guild. Although the interaction between location and dam removal was non-significant in all habitat guilds (Table 4), abundance of several guilds changed the most within the impounded reaches.

Reproductive guild abundance also differed between rivers for all guilds, except the benthic spawners (Table 4; Figure 9). Guild abundance also differed among habitats, as well as in response to dam removal in all guilds, except for the nest builders (Table 4; Figure 9). The greatest increases following dam removal were seen in the brood hiders and pelagophils. The only reproductive guild to exhibit an interaction between location and dam removal was the pelagophils (Table 4). This reproductive guild was restricted to downstream reaches of the Vermilion prior to dam removal, becoming widespread across the entire system following dam removal.

DISCUSSION

Stream Health

Consistent with past studies, conditions improved throughout both rivers following dam removal (Kanehl *et. al* 1997; Catalano *et. al* 2007; Burroughs *et. al* 2010; Butler and Wahl 2010; Dorobek *et. al* 2015). As expected in the absence of a physical barrier, flow rates increased in most locations, and water temperature decreased in both rivers following dam removal. Decreased water temperatures following dam removals are commonplace, as lacustrine environments readily stratify due to high surface area and low streamflow (Bednarek 2001; Foley *et. al* 2017). Likely associated with the combined alteration in streamflow and water temperature, dissolved oxygen levels improved substantially throughout both rivers (Gotovtsev 2010; Zhang *et. al* 2014).

QHEI scores following dam removal indicated an overall improvement in stream condition. Impounded reaches were the poorest quality habitats in both rivers and despite experiencing an increase, retained this status following dam removal. These locations may continue to improve as seasonal flows reestablish more natural conditions. Conversely, the runs of both rivers were the highest quality habitats, good to excellent, both before and after dam removal. IBI experienced a similar increase following dam removal. Improvements in IBI were driven mainly due to an increase in intolerant species and a decrease in tolerant species, particularly in the North Fork River. Such shifts in tolerant and intolerant species congruent with improved QHEI scores following dam removal is common (Hilsenhoff 1987; Kanehl et. al 1997; Stanley et. al 2002; Catalano et. al 2007). Restoration of physical habitat in the Vermilion and North Fork Vermilion Rivers likely facilitated the success of intolerant species by promoting critical habitat components of intolerant species' life history, such as spawning substrate, forage base, or shelter.

Habitat Guilds

Functional composition within both rivers in this study shifted considerably with dam removal. The greatest commonality throughout this study was the sheer prevalence of the lentic preferring guilds, particularly the slackwater guild. The high abundance of this guild prior to dam removal is unsurprising considering these fishes are characterized by an affinity to lacustrine conditions, such as those imposed by dams (Spurgeon *et. al* 2019). Following dam removals, abundance of nearly all guilds increased throughout both rivers, but the impounded regions experienced the most dramatic increases. Prior to dam removal, slackwater and habitat generalist guilds dominated impounded reaches. However, compositional diversity increased substantially following dam removal with more equal representation across guilds. Dam removal also increased compositional diversity in the downriver and run of river reaches, but to a lesser degree than impounded areas.

Stream fish assemblages are strongly dependent on physical habitat (e.g. stream depth, flow, temperature), diversifying as conditions improve (Gorman & Karr 1978; Schlosser 1982; Rahel & Hubert 1991; Catalano *et. al* 2007). Dams often degrade these conditions, particularly by accumulating sediments, leading to habitat homogenization, and eliminating distinctions between riffle, run and pool fish communities (Berkman & Rabeni 1987; Walling & Amos 1999; Collins & Walling 2007; Kemp et al. 2011). However, following dam removal, sediment transport is commonly increased (Pawloski & Cook 1993; Kanehl *et al.* 1997; Hart *et al.* 2002; Burroughs *et al.* 2010). While sediment transport was not measured in this system, it is likely to have been stimulated by the increased flow rates and connectivity. Nagayama *et al.* (2020)

documented that increased sediment transport following dam removal improved critical fish habitat and structure. Similarly, habitat conditions in my study improved throughout the rivers, increasing the abundance of lotic guilds and heterogeneity of habitat guild distribution.

Reproductive Guilds

Similar to habitat guilds, reproductive guild diversity also underwent stark transformations following dam removal. Nest builders and benthic spawners dominated both rivers prior to dam removal and remain present in large numbers even after dam removal. The nest builder guild was also the only reproductive guild that did not experience a significant increase following dam removal. Brood hiders, benthic spawners and pelagophils experienced the greatest increases following removal. This is unsurprising as dams inhibit flow and connectivity, essential to pelagophil reproduction (Durham & Wilde 2009; Mollenhauer *et al.* 2021). Dams also alter riverine habitat to become more lacustrine, resulting in sediment build up, aquatic plant growth, softer substrates, and elimination of spawning substrate needed for benthic fish reproduction (Ward & Stanford 1983; Johnson *et al.* 1995; Kemp *et al.* 2011; Keller *et al.*2021). These shifts are consistent with findings in this study, suggesting improved flow rates, habitat connectivity and quality of necessary spawning substrates for pelagohpils and benthic spawners following dam removal.

As observed with habitat guilds, heterogeneity in reproductive guilds increased, shifting from single-guild dominance to an equitable distribution of dominance across guilds. The number of unique niches available within a stream is positively associated with habitat diversity and complexity (Walrath *et. al* 2016). Because my study found stream condition, flow and dissolved oxygen improved in response to dam removal, habitat complexity also improved, driving equity in guild dominance. Although substrate was not monitored in this study, it is likely that a shift in substrate also occurred, providing an essential component of reproduction for several guilds (e.g. benthic spawners that adhere eggs to coarse substrate).

CONCLUSIONS

Although past studies examining impacts of dams using functional groups exist (Schlosser *et. al* 1982; Rahel & Hubert 1991; Smith *et. al* 2017; Oliveira *et. al* 2018), I believe utilizing guild structure is necessary approach to determine long-term community responses to disturbance, such as dam removal. This structure indicated that dam removal resulted in improved condition and functional composition within both rivers. Stream flow, dissolved oxygen levels, QHEI, and IBI scores increased substantially, fish abundance increased, and the composition of functional groups shifted to a more equitable distribution. Likely attributed to these improved conditions following removal, two fishes not previously known in Illinois have been discovered in these rivers since removal: the Tippecanoe Darter (*Nothonatus tippecanoe*) and the Streamline Chub (*Erimystax dissimilis*; Tiemann *et. al* 2021). While condition improved throughout most habitats, impounded reaches were most strongly influenced by dam removal. The immediate shifts in environmental parameters following dam removal likely catalyzed the large changes in guild composition within impounded regions. However, to assess whether spatial and temporal aspects are important to stream restoration, further monitoring is necessary. This study found that all habitat guilds benefitted from dam removal, but those associated with lotic conditions experienced far greater increases. Habitat alterations following dam removal likely led to an increased number of available niche spaces for functional groups whether assessed as habitat or reproductive guilds. Additionally, habitat and reproductive guilds shifted from single guild dominance to a more equitable distribution.

Past studies assessing dam removal indicate that immediate ecological responses to dam removal are often limited or negative (Cheng & Granata 2007; Stanley *et al.* 2007; Dorobek *et al.* 2015). Despite limited post-removal monitoring in this study, conditions of both rivers show immediate improvement following dam removal. The findings in this study emphasize the positive implications of dam removal, thus, contributing valuable knowledge to this previously limited subject. Continued monitoring of these systems is recommended to understand the long-term ecological responses of dam removal and to ensure sustained ecological improvement within these rivers.

Table 1. Results from ANOVAs examining impact of dam removal on QHEI, IBI, and environmental metrics. Significant P-values are bolded.

	df	*MS*	*F*	*P*
QHEI				
River	1	0.0005	s	0.6479
Location	2	0.1030	47.18	**P<0.0001**
Pre/Post	1	0.0070	3.21	0.0791
L x P	2	0.0071	3.25	**0.0466**
error	53	0.0022		
IBI				
River	1	0.0403	2.47	0.1202
Location	2	0.1205	7.4	**0.0012**
Pre/Post	1	0.5345	32.83	**P<0.0001**
L x P	2	0.0592	3.64	**0.0313**
error	71	0.0163		
Temperature				
River	1	0.0184	2.4	0.1257
Location	2	0.0008	0.11	0.8951
Pre/Post	1	0.1077	14.09	**0.0004**
L x P	2	0.0002	0.03	0.9681
error	71	0.0076		
Dissolved Oxygen				
River	1	0.0371	1.96	0.1658
Location	2	0.0001	0.01	0.9932
Pre/Post	1	0.3872	20.45	**P<0.0001**
L x P	2	0.0015	0.08	**0.9246**
error	71	0.0189		
Flow				
River	**1**	0.0538	14.31	**0.0004**
Location	2	0.0244	6.49	**0.003**
Pre/Post	1	0.0106	2.81	0.0993
L x P	2	0.0005	0.15	0.8653
error	53	0.0038		

Table 2. Results of PERMANOVA's examining impacts of dam removal on habitat and reproductive guild abundances. Significant P-Values are bolded.

	df	*Mean Square*	R^2	*F*	*P*
Habitat Guilds					
River	1	0.7144	0.1394	15.2459	**P<0.0001**
Location	2	0.1687	0.0658	3.5989	**0.0025**
Pre/Post	1	0.5959	0.1163	12.7175	**P<0.0001**
L x P	2	0.0744	0.0291	1.5893	0.1424
error	71	0.0469	0.6494		
Reproductive Guilds					
River	1	0.4522	0.0980	11.1144	**P<0.0001**
Location	2	0.1720	0.0746	4.2288	**0.0006**
Pre/Post	1	0.7722	0.1673	18.9795	**P<0.0001**
L x P	2	0.0787	0.0341	1.9341	0.0720
error	71	0.0407	0.6260		

Table 3. ANOVA results assessing the impact of dam removal on habitat and reproductive guild diversity. Significant P-values are bolded.

	df	*Mean Square*	*F*	*P*
Habitat Guilds				
River	1	0.494	6.74	**0.0115**
Habitat	2	0.615	8.40	**0.0005**
Pre/Post	1	1.197	16.33	**0.0001**
L x P	2	0.197	2.67	0.0750
error	71	0.073		
Reproductive Guilds				
River	1	0.004	0.06	0.8007
Habitat	2	0.426	7.10	**0.0015**
Pre/Post	1	1.742	29.06	**P<0.0001**
L x P	2	0.300	5.01	**0.0092**
error	71	0.060		

Table 4. Results of ANOVAs examining impacts of dam removal on abundances of each guild. Significant P-values are bolded.

	df	*MS*	*F*	*P*
Habitat Generalist				
River	1	5.21	27.77	**P<0.0001**
Location	2	1.01	5.41	**0.0065**
Pre/Post	1	6.38	34.01	**P<0.0001**
L x P	2	0.56	2.97	0.0578
error	71	0.19		
Lobate Margin				
River	1	18.67	46.02	**P<0.0001**
Location	2	1.76	4.35	**0.0166**
Pre/Post	1	1.77	4.36	**0.0403**
L x P	2	1.01	2.48	0.0910
error	71	0.41		
Riffle				
River	1	7.32	15.56	**0.0002**
Location	2	4.39	9.33	**0.0003**
Pre/Post	1	12.73	27.06	**P<0.0001**
L x P	2	0.97	2.07	0.1337
error	71	0.47		
Run				
River	1	0.01	0.00	0.9978
Location	2	2.06	6.44	**0.0027**
Pre/Post	1	11.93	37.35	**P<0.0001**
L x P	2	0.98	3.07	0.0525
error	71	0.32		
Slackwater				
River	1	3.44	14.81	**0.0003**
Location	2	0.97	4.16	**0.0197**
Pre/Post	1	0.38	1.62	0.2070
L x P	2	0.14	0.61	0.5474
error	71	0.23		
Benthic Spawner				
River	1	0.36	1.43	0.2365
Location	2	1.15	4.55	**0.0138**
Pre/Post	1	5.48	21.71	**P<0.0001**
L x P	2	0.66	2.61	0.0808
error	71	0.25		
Brood Hider				
River	1	4.40	10.36	**0.0019**
Location	2	3.99	9.38	**0.0002**
Pre/Post	1	15.08	35.50	**P<0.0001**
L x P	2	1.07	2.52	0.0874
error	71	0.43		
Nest Builder				
River	1	8.44	32.70	**P<0.0001**
Location	2	0.50	1.93	0.1534
Pre/Post	1	0.48	1.86	0.1764
L x P	2	0.08	0.30	0.7394
error	71	0.26		
Pelagophil				
River	1	5.86	24.14	**P<0.0001**
Location	2	1.32	5.42	**0.0064**
Pre/Post	1	12.09	49.78	**P<0.0001**

L x P	2	1.13	4.64	**0.0128**
error	71	0.24		

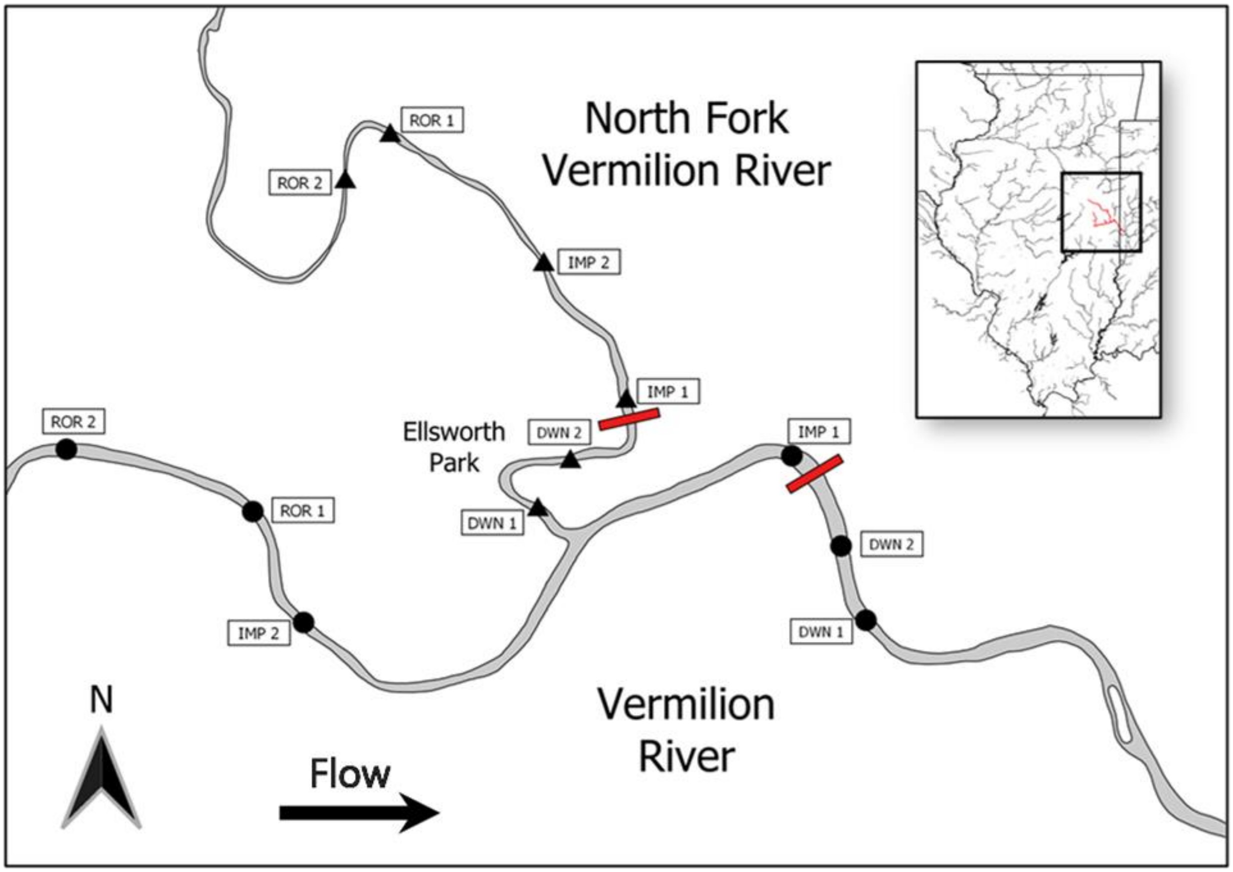

Figure 1. Map of sample sites on the Vermilion and North Fork Rivers . Circles indicate sites on the Vermilion River, triangles represent site on the North Fork River and the red bars indicate the dam removal sites. DWN : Downriver of Dam, IMP: Impounded, ROR: Run of River.

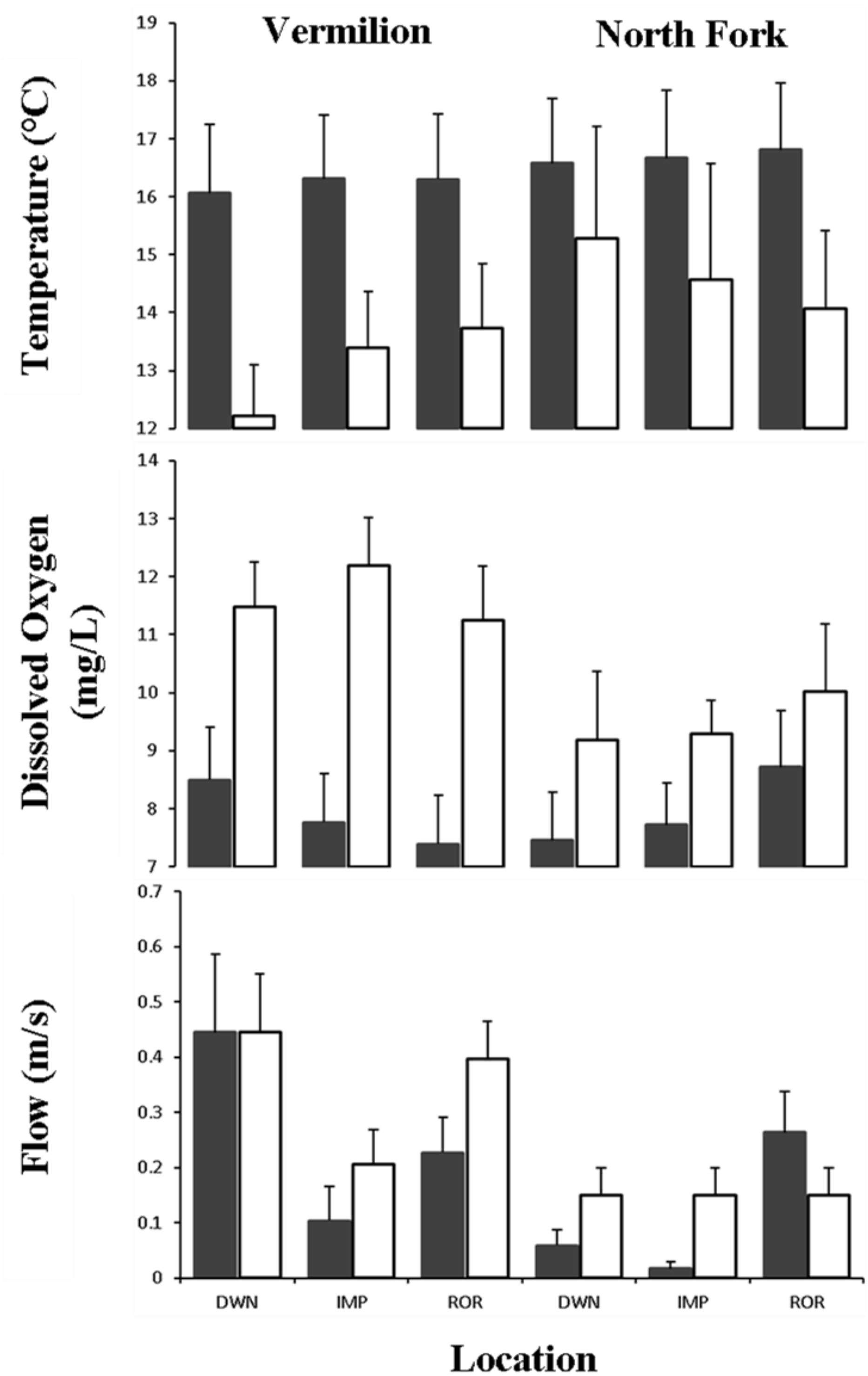

Figure 2. Response of environmental parameters to river location and dam removal. Grey indicate pre-removal values and white indicate post-removal values. Values plotted are means +/- standard error. Refer to Figure 1 for explanation of location abbreviations.

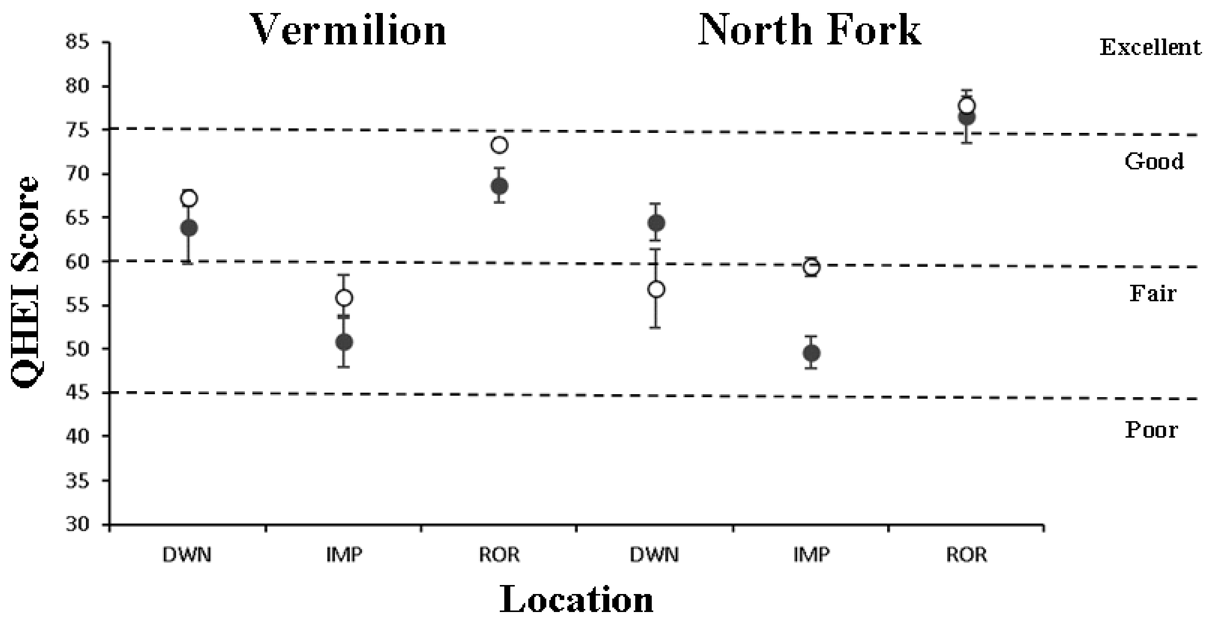

Figure 3. Response of QHEI to river location and dam removal of each habitat on both rivers. Grey markers are average pre-removal values and white markers are average post-removal, +/- standard error. Dashed lines are labeled to correspond score to the health of the river. Refer to Figure 1 for explanation of location abbreviations.

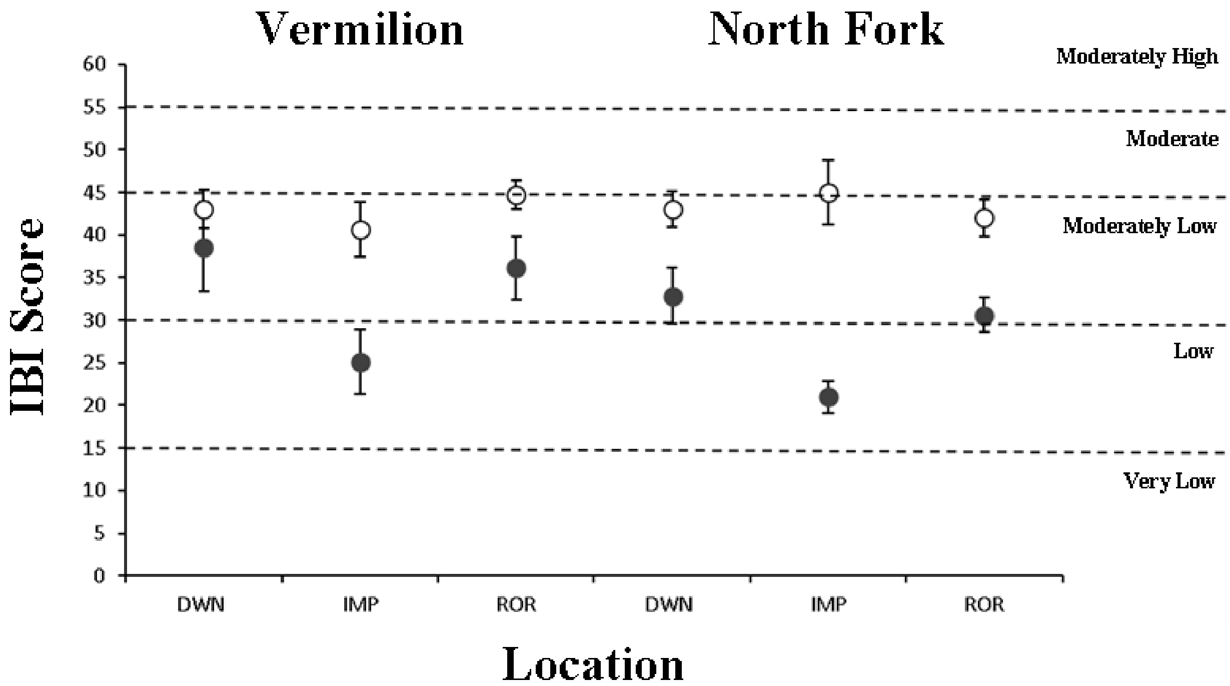

Figure 4. Response of Index of Biotic Integrity (IBI) to river location and dam removal of each habitat on both rivers. Grey markers are average pre-removal values and white markers are average post-removal, +/- standard error. Dashed lines are labeled to correspond score to the health of the river. Refer to Figure 1 for explanation of location abbreviations.

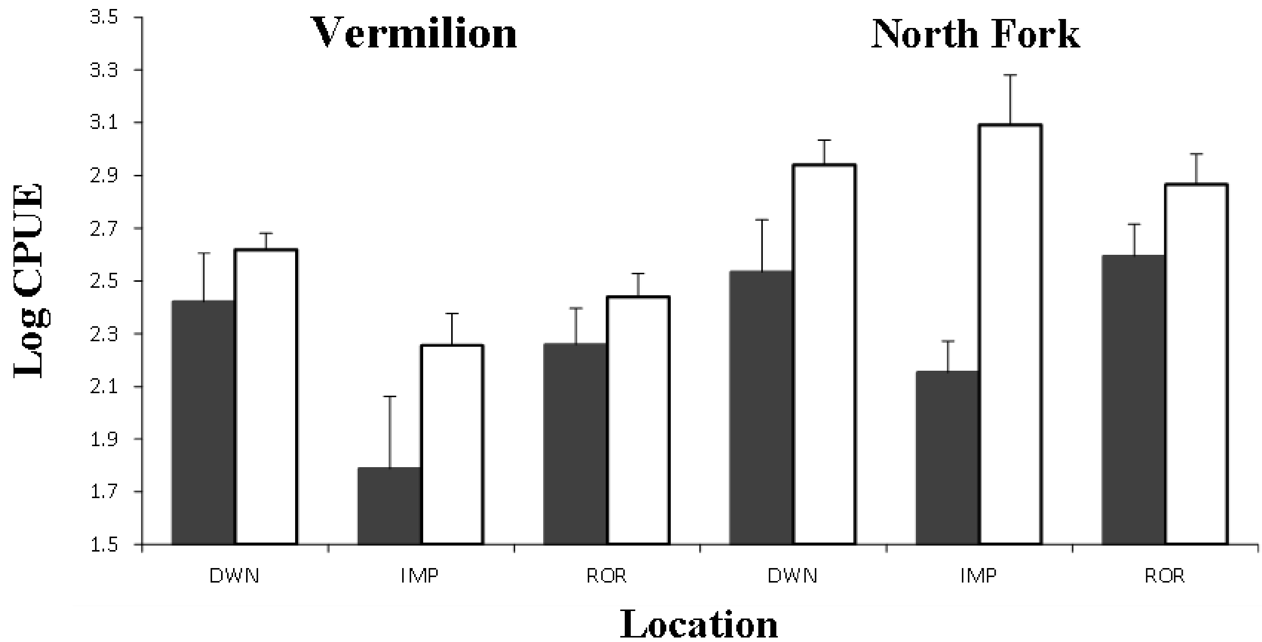

Figure 5. Response of total fish abundances to dam removal in each river location. Grey bars indicate pre-removal values and white bars indicate post-removal values. Values plotted are means +/- standard error. Refer to Figure 1 for explanation of location abbreviations.

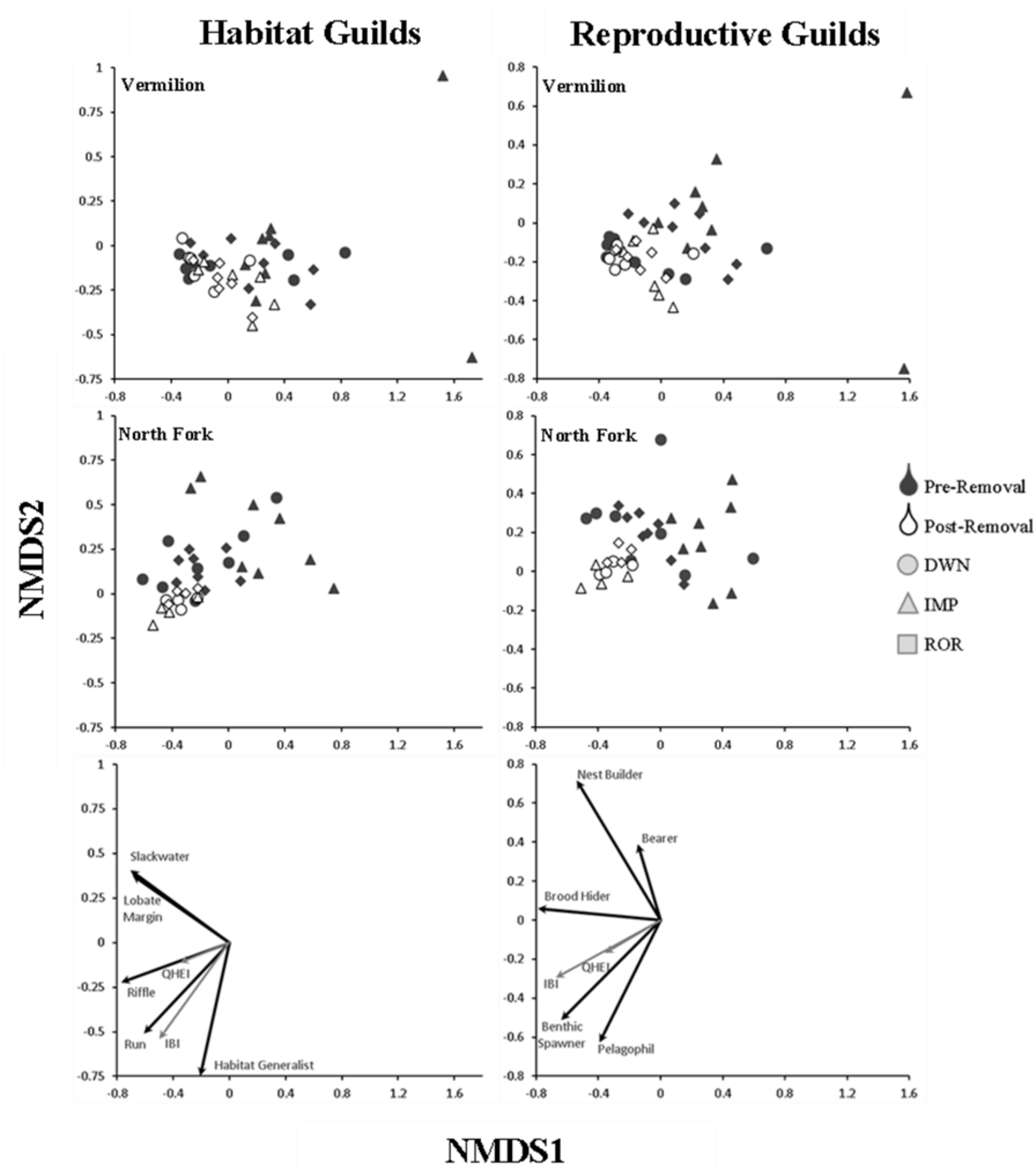

Figure 6. Non-metric multidimensional scaling (NMDS) ordination displaying impacts of dam removal on habitat and reproductive guild abundances and habitat metrics. Guilds are displayed as black vectors and QHEI and IBI are displayed as a grey vectors. Refer to Figure 1 for explanation of location abbreviations.

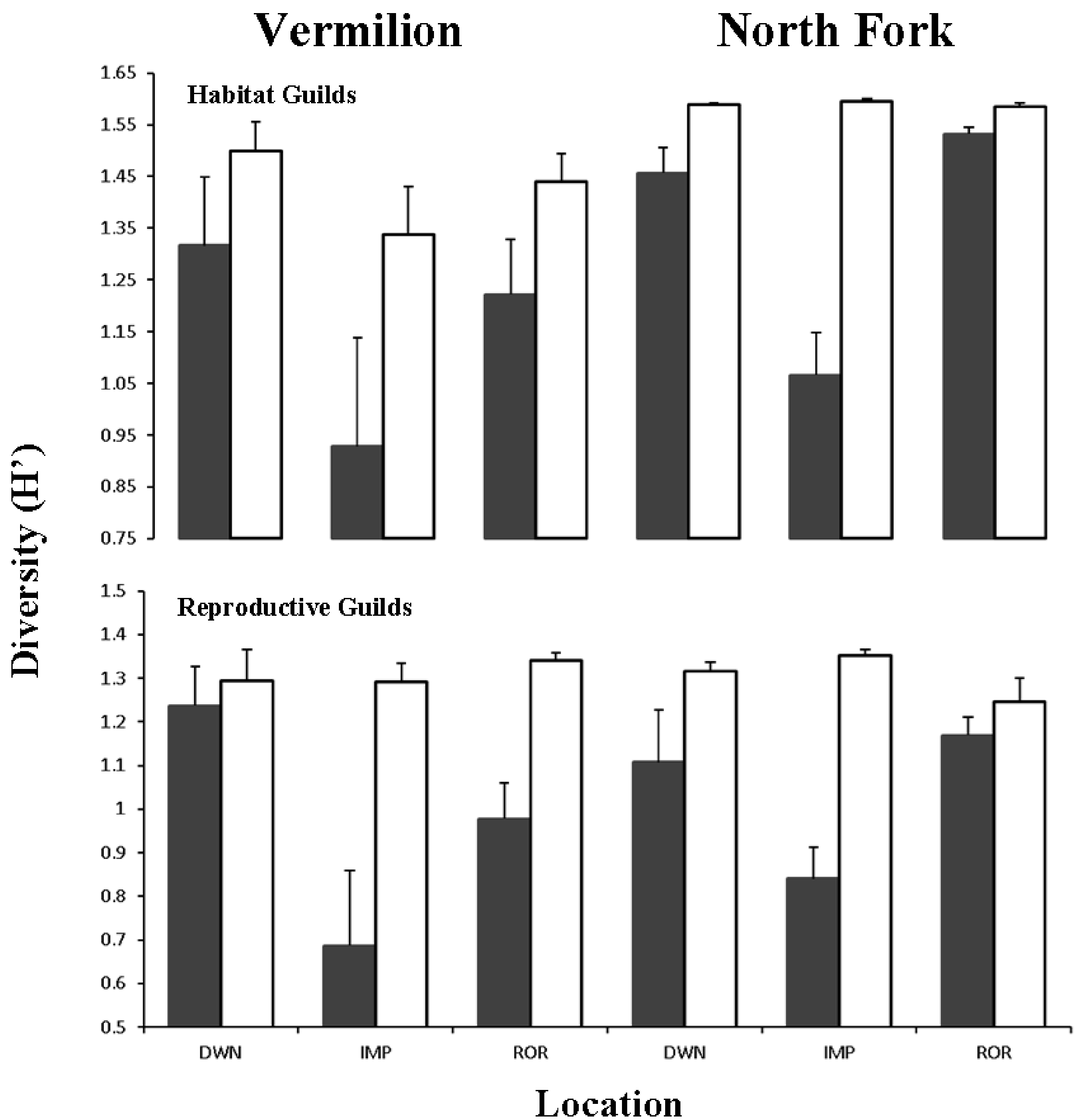

Figure 7. Response of guild diversity to dam removal. Grey bars indicate pre-removal values and white bars indicate post-removal values. Values plotted are means +/- standard error. Refer to Figure 1 for explanation of location abbreviations.

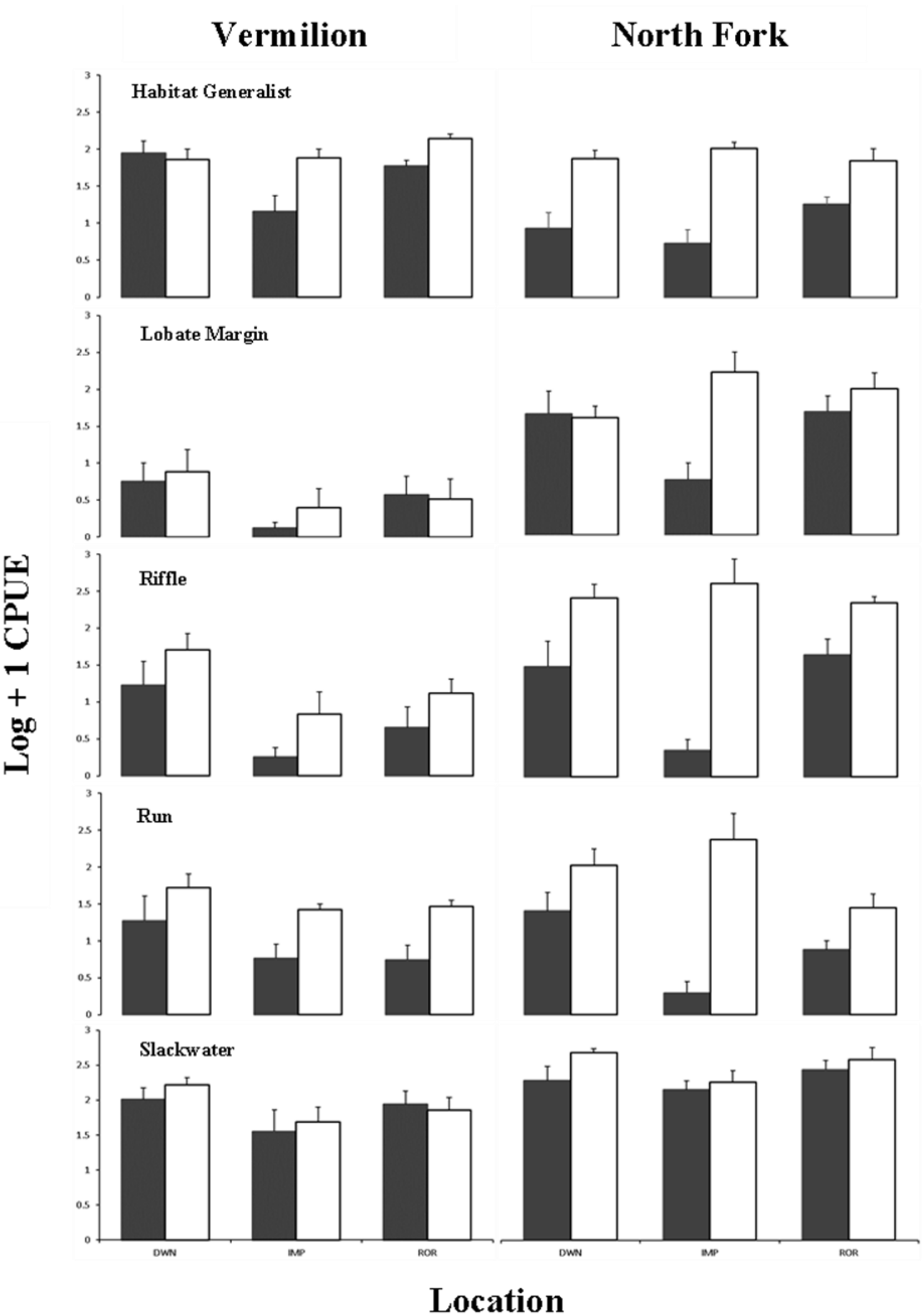

Figure 8. Response of habitat guild abundances to river location and dam removal. Grey bars indicate pre-removal values and white bars indicate post-removal values. Values plotted are means +/- standard error. Refer to Figure 1 for explanation of location abbreviations.

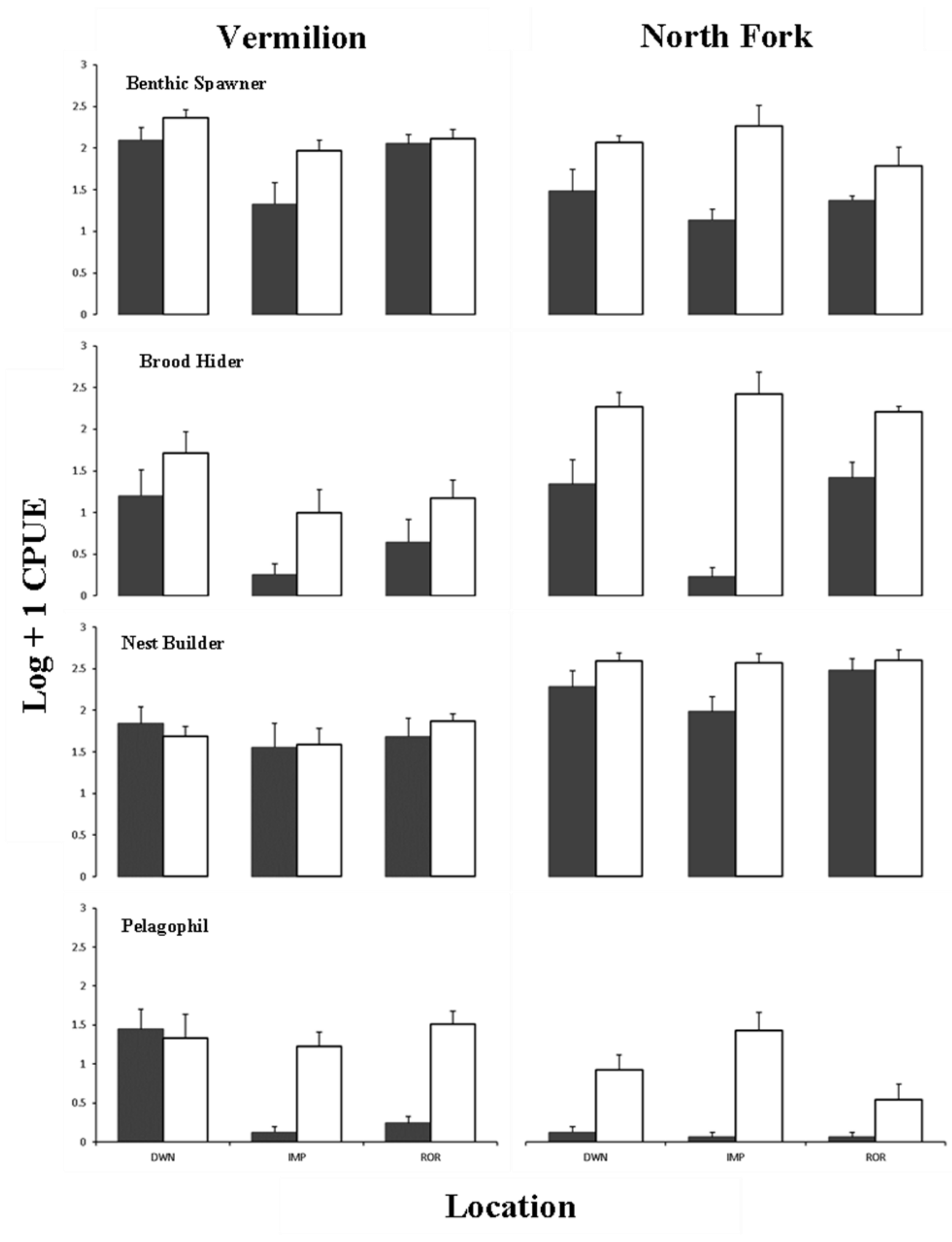

Figure 9. Response of reproductive guild abundances to river location and dam removal. Grey bars indicate pre-removal values and white bars indicate post-removal values. Values plotted are means +/- standard error. Refer to Figure 1 for explanation of location abbreviations.

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APPENDIX A: ADDITIONAL FIGURES

Table A 1. List of species aggregated into habitat and reproductive guilds.

Species	*Habitat Guild*	*Reproductive Guild*
Amiidae		
Bowfin	Slackwater	Nest Builder
Aphredoderidae		
Pirate Perch	Lobate Margin	Benthic Spawner
Atherinopsidae		
Brook Silverside	Lobate Margin	Benthic Spawner
Catostomidae		
Bigmouth Buffalo	Slackwater	Benthic Spawner
Black Buffalo	Slackwater	Benthic Spawner
Black Redhorse	Habitat Generalist	Benthic Spawner
Golden Redhorse	Habitat Generalist	Benthic Spawner
Highfin Carpsucker	Slackwater	Benthic Spawner
Northern Hog Sucker	Habitat Generalist	Benthic Spawner
Quillback	Habitat Generalist	Benthic Spawner
River Carp Sucker	Habitat Generalist	Benthic Spawner
River Redhorse	Habitat Generalist	Benthic Spawner
Shorthead Redhorse	Habitat Generalist	Benthic Spawner
Silver Redhorse	Habitat Generalist	Benthic Spawner
Smallmouth Buffalo	Slackwater	Benthic Spawner
Spotted Sucker	Slackwater	Benthic Spawner
White Sucker	Habitat Generalist	Benthic Spawner
Centrarchidae		
Black Crappie	Slackwater	Nest Builder
Bluegill	Slackwater	Nest Builder
Green Sunfish	Slackwater	Nest Builder
Largemouth Bass	Slackwater	Nest Builder
Longear Sunfish	Slackwater	Nest Builder
Orangespotted Sunfish	Habitat Generalist	Nest Builder
Rockbass	Habitat Generalist	Nest Builder
Smallmouth Bass	Run	Nest Builder
Spotted Bass	Run	Nest Builder
Warmouth	Slackwater	Nest Builder
White Crappie	Slackwater	Nest Builder
Clupeidae		
Gizzard Shad	Slackwater	Benthic Spawner
Skipjack Herring	Run	Benthic Spawner
Cyprinidae		
Bigeye Chub	Habitat Generalist	Benthic Spawner
Bluntnose Minnow	Lobate Margin	Nest Builder
Bullhead Minnow	Lobate Margin	Nest Builder
Central Stone Roller	Riffle	Brood Hider
Common Carp	Slackwater	Benthic Spawner
Creek Chub	Habitat Generalist	Brood Hider
Emerald Shiner	Run	Pelagophil
Golden Shiner	Habitat Generalist	Benthic Spawner
Grass Carp	Slackwater	Pelagophil
Hornyhead Chub	Habitat Generalist	Brood Hider
Largescale Stoneroller	Riffle	Brood Hider
Mimic Shiner	Riffle	Benthic Spawner
Red Shiner	Lobate Margin	Brood Hider
Redear Sunfish	Slackwater	Nest Builder
Redfin Shiner	Habitat Generalist	Benthic Spawner
River Shiner	Riffle	Benthic Spawner
Rosyface Shiner	Riffle	Brood Hider
Sand Shiner	Run	Benthic Spawner
Silver Carp	Habitat Generalist	Pelagophil
Silver Chub	Lobate Margin	Benthic Spawner

Silver Jaw Minnow	Lobate Margin	Benthic Spawner
Silvery Minnow	Run	Benthic Spawner
Spotfin Shiner	Riffle	Brood Hider
Steelcolor Shiner	Riffle	Brood Hider
Streamline Chub	Riffle	Benthic Spawner
Striped Shiner	Run	Brood Hider
Suckermouth Minnow	Riffle	Benthic Spawner
Esocidae		
Grass Pickerel	Slackwater	Benthic Spawner
Fundulidae		
Blackstripe Topminnow	Lobate Margin	Benthic Spawner
Hiodontidae		
Goldeye	Habitat Generalist	Benthic Spawner
Mooneye	Slackwater	Benthic Spawner
Ictaluridae		
Brindled Madtom	Riffle	Nest Builder
Channel Catfish	Habitat Generalist	Nest Builder
Flathead Catfish	Habitat Generalist	Nest Builder
Freckled Madtom	Riffle	Nest Builder
Stonecat	Riffle	Nest Builder
Tadpole Madtom	Lobate Margin	Nest Builder
Yellow Bullhead	Slackwater	Nest Builder
Lepisosteidae		
Shortnose Gar	Habitat Generalist	Benthic Spawner
Spotted Gar	Slackwater	Benthic Spawner
Moronidae		
White Bass	Slackwater	Benthic Spawner
Yellow Bass	Slackwater	Benthic Spawner
Percidae		
Bluebreast Darter	Riffle	Benthic Spawner
Dusky Darter	Riffle	Brood Hider
Eastern Sand Darter	Run	Benthic Spawner
Fantail Darter	Riffle	Nest Builder
Greenside Darter	Riffle	Benthic Spawner
Johnny Darter	Habitat Generalist	Brood Hider
Log Perch	Riffle	Brood Hider
Orangethroat Darter	Riffle	Brood Hider
Rainbow Darter	Riffle	Brood Hider
Sauger	Slackwater	Benthic Spawner
Saugeye	Slackwater	Benthic Spawner
Slenderhead Darter	Riffle	Brood Hider
Walleye	Slackwater	Benthic Spawner
Petromyzontidae		
Chestnut Lamprey	Run	Brood Hider
Poeciliidae		
Mosquito Fish	Lobate Margin	Bearer
Sciaenidae		
Freshwater Drum	Habitat Generalist	Pelagophil