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

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Abstract

Despite the growing number of dam removals, very few have been studied to understand their impacts on stream fish communities. An even smaller proportion of dam removal studies focus on the impacts of low-head dam removals, although they are the most common type of dam. Instead, the majority of removal studies focus on the impacts 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. Study sites were sampled each fall from 2012-2015 (pre-dam removal) and 2018-2020 (post-dam removal) in three habitat types: downstream of the dam, impounded areas, and runs of rivers. Fishes were aggregated 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. During the two years 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 habitat and reproductive guilds. The improvements in environmental metrics and overall stream quality, particularly in the formerly 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 inhabiting these rivers, while simultaneously preventing single-guild dominance.

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ABSTRACT

Despite the growing number of dam removals, very few have been studied to understand their impacts on stream fish communities. An even smaller proportion of dam removal studies focus on the impacts of low-head dam removals, although they are the most common type of dam. Instead, the majority of removal studies focus on the impacts 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. Study sites were sampled each fall from 2012-2015 (pre-dam removal) and 2018-2020 (post-dam removal) in three habitat types: downstream of the dam, impounded areas, and runs of rivers. Fishes were aggregated 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. During the two years 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 habitat and reproductive guilds. The improvements in environmental metrics and overall stream quality, particularly in the formerly 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 inhabiting these rivers, while simultaneously preventing single-guild dominance.

KEY WORDS: low-head dam; dam removal; reproductive guilds; habitat guilds; diversity; functional composition; habitat restoration

INTRODUCTION

To date, more than 1,400 dams have been removed from U.S. waterways (American Rivers 2019), however, less than 10% of removals have been studied to understand their impacts on stream fishes (Bellmore *et al.* 2017). Stream fishes are often particularly vulnerable to the ecological impacts imposed by dams (Oliveira *et al.* 2018; Turgeon*et al.* 2019; Barbarossa *et al.* 2020), often resulting in significant shifts in community composition, such as an increase in homogenization of assemblages in streams with the higher spring flow (Hastings *et al.* 2016). Such changes in fish communities may arise from many drivers, 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 dominance of fishes adapted to lentic conditions and those possessing a high degree of functional plasticity, as they are capable of inhabiting lacustrine conditions (Agostinho *et al.* 2008; Turgeon *et al.* 2019). As sufficient plasticity and tolerance is not common in fishes, reductions in diversity and abundance are often associated with impounded systems (Agostinho *et al.* 2008; Turgeon *et al.*2019).

Although dam removals are often motivated by dam age and degradation that diminish utility (Doyle *et al.* 2003), increased public awareness of the ecological costs imposed by dams and the desire to restore rivers to a more natural state are also driving forces (Bednarek 2001; Poulos *et al.* 2014; Poulos & Chernoff 2016). Despite the intent to restore the system, successful outcomes are uncertain (e.g., Cheng & Granata 2007; Stanley *et al.* 2007; Chang *et al.*2016). For example, dam removal 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 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). Very few studies have focused on low-head dams (no higher than 9 m) although they make up the majority of dams in the U.S. (USACE NID 2018; Iowa Department of Natural Resources 2021). Within the limited studies on low-head dams, few analyze the impacts of removal and the responses of stream fish communities (Bellmore *et al.* 2017). Rather, these studies focus on understanding the effects on stream fishes and the environment in response to the presence of dams (Butler & Wahl 2010; Alexandre & Alemida 2010; Smith *et al.* 2017). With the increasing rate of removals (Poff & Hart 2002), improved understanding of how low-head dam removal affects stream fish assemblages is imperative.

Although a few studies document low-head dam removal and their effects on fishes (Burdick & Hightower 2006; Catalano *et al.* 2007; Cook & Sullivan 2018), an even smaller proportion analyze functional impacts on stream fish communities by examining guilds (Dorobek *et al.*2015; Ding *et al.* 2019). Functional guilds can serve as indicators of community response to variations in a river's hydrology, geomorphology, and habitat structure (Welcomme *et al.* 2006). Because many of the factors used to aggregate fishes into guilds are often impacted by dam presence and removal, changes in guild structure should provide functional understanding. This approach emphasizes connections between 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. Despite its potential, use of a guild structure may be complicated by limited data, intraspecific variation, and ontogenetic shifts in functional traits (Benoit *et al.* 2021). Regardless, a guild structure offers an innovative and versatile method to increase our understanding of stream fish community dynamics (Benoit *et al.* 2021).

While guilds provide an assessment of functional composition, understanding environmental relationships may be strengthened by the simultaneous use of additional metrics. 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, we utilized habitat and reproductive guilds to analyze changes in the fish communities of two Illinois streams in response to low-head dam removal. To accomplish this, we analyzed fish and habitat data collected over 7 years; 4 years of pre-removal data (Hastings *et al.* 2015, 2016; Smith *et al.* 2017) and 3 years of post-removal data, in an effort to; (i) document immediate habitat and stream fish responses to low-head dam removal (ii) document functional changes in stream fishes in response to low-head dam removal and (iii) identify relationships between environmental and stream fish responses. We expected that overall health of the rivers would improve, with increased flow rates and dissolved oxygen in response to dam removal, but the greatest improvements would occur in the impounded reaches. We also predicted that dominance of lacustrine-adapted fishes would decrease, increasing functional group diversity 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 located in Danville since the early 1900s, 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. 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 at six study sites within each river, each measuring 100 m in length. The six sites within each river 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 sampling occurred in the fall of 2012-2015 and post-removal sampling 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

Fish collection was conducted using DC electrofishing methods as described in Hastings *et al.* (2015); by boat on the Vermilion River and barge on the North Fork Vermilion River, where waters levels were too shallow for boat navigation, except in 2014 and 2015 where elevated water levels required boat electrofishing. Each site was sampled for 30 minutes, and fish were identified to species, weighed (g) and measured (total length, mm) after each effort. Any specimen with a total length below 100 mm was not weighed, and those that were not easily identified in the field (e.g., *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, these species were photographed and released; photographs were later examined to count lateral line scales to distinguish these 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 via 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. Metric 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, similar to QHEI, summed to compute an overall score (Smogor 2000).

Water quality was also measured at 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 variables assessed include surface water velocity (m/s) in the middle of the channel (Hach Portable Velocity Meter; Hach Company, Loveland, CO), turbidity (m; Secchi board), and stream width (m).

Guild Assignment

Five habitat guilds were constructed following Spurgeon *et al.*(2019) and literature (Pflieger 1997; Page & Burr 2011): lobate margin, run, riffle, slackwater and habitat generalist (Table A1). The lobate margin guild was described as including fishes that inhabit areas of low velocity and shallow depths on channel margins. The run guild included 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 were those preferring off channel pools or backwaters near stream edges. Finally, habitat generalist fishes were those that are not associated with a specific habitat type and are found in several types of habitats (Spurgeon *et al* . 2019).

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 (Table A1). 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, all 'guarder' sub-groups described by Balon (1975, 1981) and Simon (1999) were included as 'nest builders' in our study.

Data Analysis

Data used for each analysis consisted of catch per unit effort (CPUE; fish/hr) using species abundance aggregated into habitat and reproductive guilds. The resulting CPUE values were log + 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 to address zeros in the data set. Two-way analysis of variance (ANOVA), followed by Tukey's honest significant difference (HSD) post-hoc tests, were used to determine impacts of dam removal (pre- and post-removal) and habitat (downstream of dam, impounded, run of river) that may explain trends in functional composition, QHEI, IBI, environmental variables and overall species abundances. River was included as a blocking variable to control for variation between the two systems. Significant factors were subsequently tested to identify differences using a Tukey HSD test.

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-Wiener diversity index (Shannon and Weaver, 1949), and abundance of each functional group were analyzed using two-way ANOVAs as described above. Diversity was calculated using the same log + 1 transformed data described in the NMDS ordination above and CPUE of each functional group was calculated. Live bearers were omitted from the abundance analysis because of low occurrence in the dataset. R version 3.6 (R Foundation for Statistical Computing) was 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 parameter 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; Figure 4). QHEI overall increased following dam removal but the changes were largest in impounded reaches, resulting in a significant location × removal interaction (Table 1; Figure 3). Similarly, IBI increased following dam removal in all sites, but impounded regions experienced greater improvements than 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) increasing at all sites, particularly in the impounded reaches. Abundance of fishes also responded to location (ANOVA $F_{2,71} = 5.29$, $P = 0.007$), with abundance being lowest in the impounded reaches. Although abundance increased most substantially in the impounded reaches, there was no location by removal interaction (ANOVA $F_{2,71} = 1.74$, $P = 0.182$). Abundance also differed between rivers (ANOVA $F_{1,71} = 11.24$, $P = 0.001$) and were overall higher in the North Fork Vermilion.

Functional Assemblages and Guild Diversity

There was a clear impact of dam removal on habitat guild composition in both rivers as well as compositional differences between rivers and among locations, which can be visualized in the NMDS ordination on habitat guild composition (Table 2; Figure 6). In both rivers dam removal resulted in a marked negative shift on NMDS1, reflecting the decrease in slackwater and lobate margin guilds, and an increase in riffle, run and habitat generalist guilds. Homogeneity of habitat guild composition increased across all sites following dam removal. (Figure 6).

Reproductive guild composition within both rivers was clearly impacted by dam removal (Table 2: Figure 6). 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 (Figure 6). 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. Dam removal resulted in a general negative shift along NMDS1 reflecting an increase in benthic spawners and brood hiders with pelagophils also influencing the shift to a lesser degree. Reproductive guild composition became more homogenous across all habitats following dam removal (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 independent from nest builders and live bearers. Guilds associated with QHEI were similarly associated with IBI, however these relationships were stronger. Within reproductive guilds, QHEI and IBI were nearly identical in their guild relationships. Both QHEI and IBI reflected the compositional changes associated with dam removal, regardless of guild type.

Diversity of habitat and reproductive guilds increased following dam removal by location (Table 3; Figure 7). Effects of dam removal varied significantly by location in both guild types, however, only habitat guild diversity differed between rivers, with higher diversity in the North Fork Vermilion. While increases in the diversity of both guild types were 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 based on their habitat preferences and all guilds, except the run guild, differed between rivers (Table 4; Figure A1). Dam removal increased the abundance of all habitat guilds, except for the slackwater guild which did not change. Although the interaction between location and dam removal was non-significant in all habitat guilds, abundance of all guilds, except slackwater, increased most substantially within the impounded reaches.

Reproductive guild abundance differed between rivers for all guilds, except benthic spawners (Table 4; Figure A2). Abundance of all guilds, except nest builders, differed among habitats and in response to dam removal, with the greatest increases occurring in the impounded reaches for these guilds. Brood hiders and pelagophils experienced the greatest increases in abundance following dam removal. Additionally, the only reproductive guild to exhibit an interaction between location and dam removal was the pelagophils, which were restricted to the downstream reaches of the Vermilion prior to dam removal but became widespread across the entire system following dam removal (Table 4; Figure A2).

DISCUSSION

Stream Health

Consistent with past studies, ecological and habitat 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). Although not significantly different, flow rates increased in most locations following dam removal, as would be expected in the absence of a physical barrier. Water temperature decreased in both rivers following dam removal. This is commonplace in dam removals, 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 increased 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 pre-removal 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 both before and after dam removal. IBI experienced a similar increase following dam removal. Improvements in IBI were driven mainly by an increase in intolerant species (e.g., Smallmouth Bass, Spotted Bass, Spotted Sucker, Black Redhorse) and a decrease in tolerant species(e.g., Green Sunfish, Golden Redhorse) particularly in the North Fork Vermilion River. Such shifts in tolerant and intolerant species congruent with improved QHEI scores following dam removal are common (Hilsenhoff 1987; Kanehl *et al.* 1997; Stanley *et al.* 2002; Catalano *et al.* 2007). Restoration of physical habitat (i.e., natural flow regime) 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. Prior to removal, lentic-preferring guilds were most prevalent throughout this system, 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). 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 connectivity. Nagayama *et al.* (2020) documented that increased sediment transport following dam removal improved critical fish habitat and structure. Similarly, habitat conditions in the current 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 the 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, finer 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 our findings, suggesting improved flow rates, habitat connectivity and quality of necessary spawning substrates for pelagophils 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 the current study found stream condition and dissolved oxygen improved in response to dam removal, habitat complexity also may have improved, driving equity in guild presence. 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

Dam removals are often approached with hesitance due to perceived losses of some fish species and the potential for adverse environmental impacts (Bednarek 2001; Hart*et al.* 2002; Downs *et al.* 2011; Magilligan *et al.*2017). However, this system experienced immediate improvements in stream flow, dissolved oxygen levels, QHEI scores, IBI scores, and fish abundance. Rather than decreases in some functional groups, abundances of most increased following removal. The increase in less abundant functional groups resulted in greater equivalence across all functional groups, increasing the functional diversity of the fish assemblage as a result. Although past studies indicate that immediate ecological responses to dam removal can be limited or negative (Cheng & Granata 2007; Stanley *et al.* 2007; Dorobek *et al.* 2015), improvements in the functional diversity, overall abundance and habitat observed in our study following dam removal show no potential downside of dam removal. In fact, two fishes not previously found in Illinois have been discovered in these rivers since removal, likely in response to improved conditions: the Tippecanoe Darter (*Nothonatus tippecanoe*) and the Streamline Chub (*Erimystax dissimilis* ; Tiemann *et al.* 2021). Despite the immediate improvements, we recommend continued monitoring of these systems to ensure sustained restoration and to improve our understanding of long-term ecological responses to dam removal.

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Table . 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 (°C)	Temperature (°C)			
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(mg/L)	Dissolved Oxygen(mg/L)			
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 (m/s)				
River	**1**	0.0538	14.31	**0.0004**

	df	*MS*	*F*	*P*
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	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 (H'). Significant P-values are bolded.

	df	*Mean Square*	*F*	*P*
Habitat Guild Diversity	Habitat Guild Diversity			
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 Guild Diversity	Reproductive Guild Diversity			
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**

	df	*MS*	*F*	*P*
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**

	df	*MS*	*F*	*P*
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.

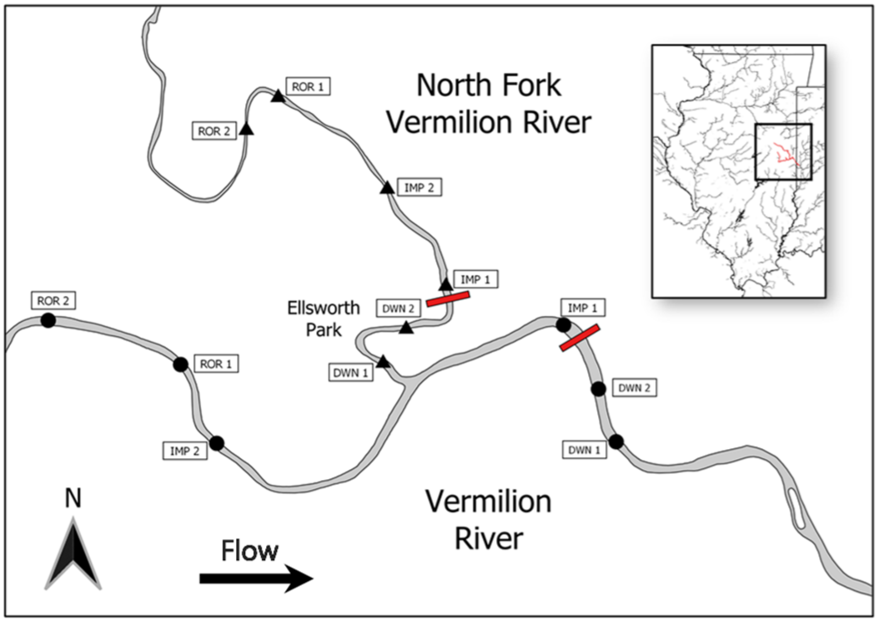
Figure 6. Non-metric multidimensional scaling (NMDS) ordination displaying impacts of dam removal on habitat and reproductive guild abundances and habitat metrics. Guilds are displayed as black vectors and QHEI and IBI are displayed as a grey vectors. Refer to Figure 1 for explanation of location abbreviations.

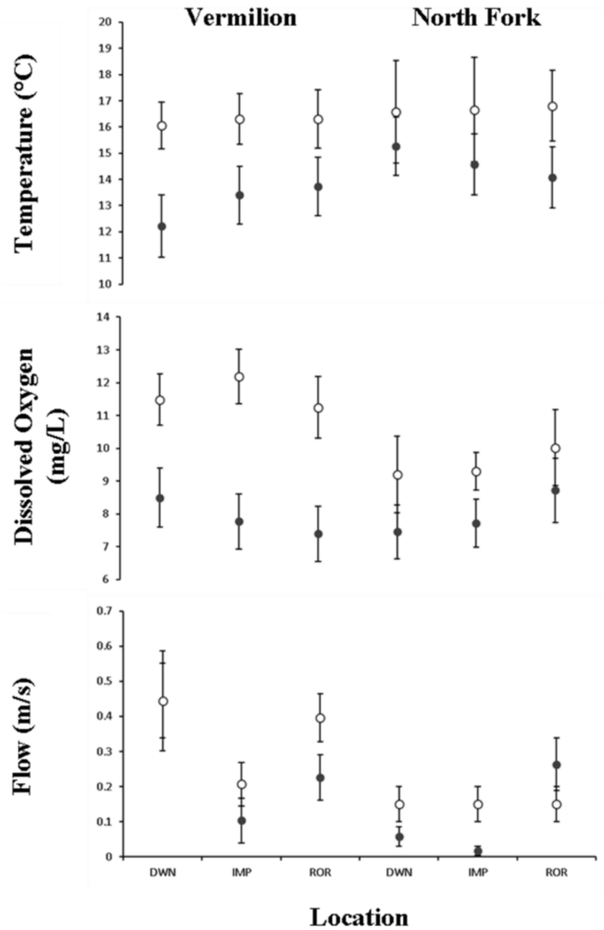
Figure 7. Response of guild diversity to dam removal. Grey bars indicate pre-removal values and white bars indicate post-removal values. Values plotted are means +/- standard error. Refer to Figure 1 for explanation of location abbreviations.

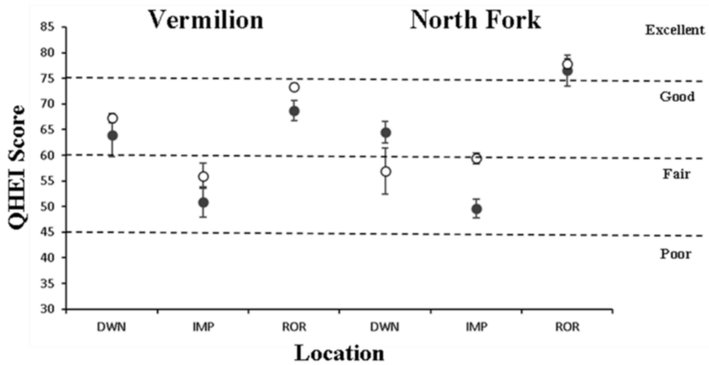
APPENDIX A: ADDITIONAL FIGURES

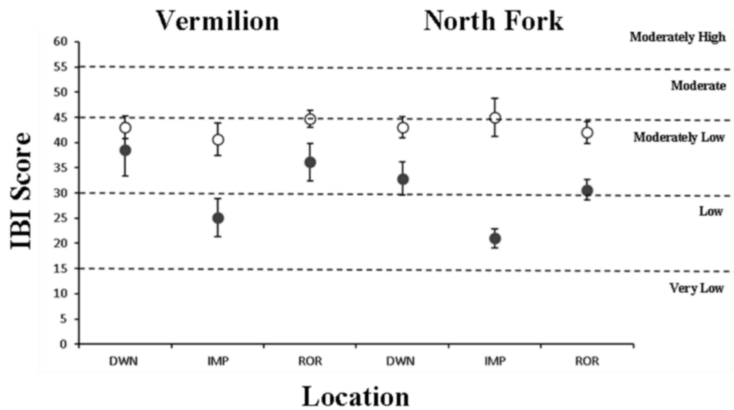
Figure A1. Response of habitat guild abundances to river location and dam removal. Grey bars indicate pre-removal values and white bars indicate post-removal values. Values plotted are means +/- standard error. Refer to Figure 1 for explanation of location abbreviations.

Figure A2. 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.


North Fork
Vermilion River
ROR 1
ROR 2
IMP 2
IMP 1
DWN 2
DWN 1
Ellsworth
Park
ROR 2
ROR 1
IMP 2
IMP 1
DWN 2
DWN 1
Vermilion
River
N
Flow


Vermilion
North Fork
Temperature (°C)
Dissolved Oxygen (mg/L)
Flow (m/s)
DWN
IMP
ROR
DWN
IMP
ROR
Location


Vermilion
North Fork
Excellent
Good
Fair
Poor
QHEI Score
85
80
75
70
65
60
55
50
45
40
35
30
DWN
IMP
ROR
DWN
IMP
ROR
Location


Vermilion
North Fork
IBI Score
Moderately High
Moderate
Moderately Low
Low
Very Low
60
55
50
45
40
35
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25
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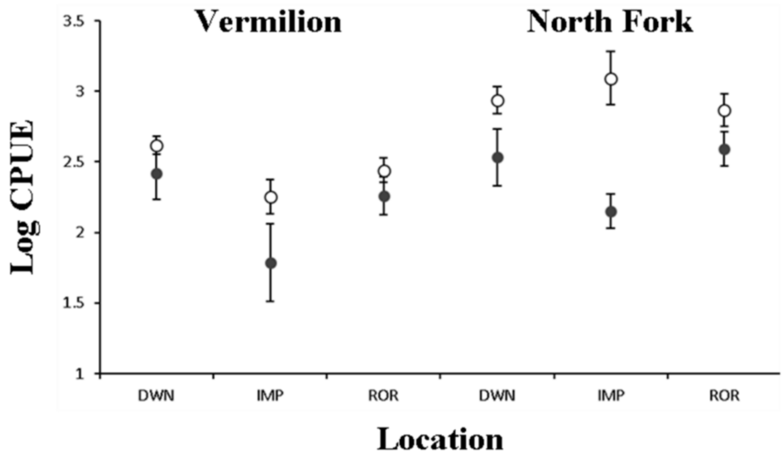
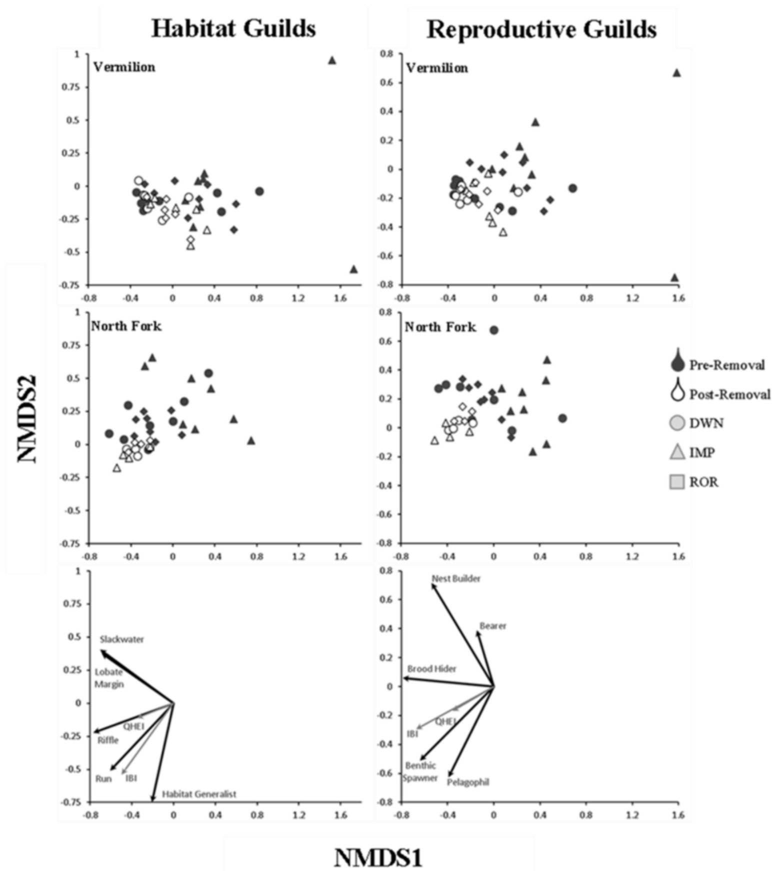
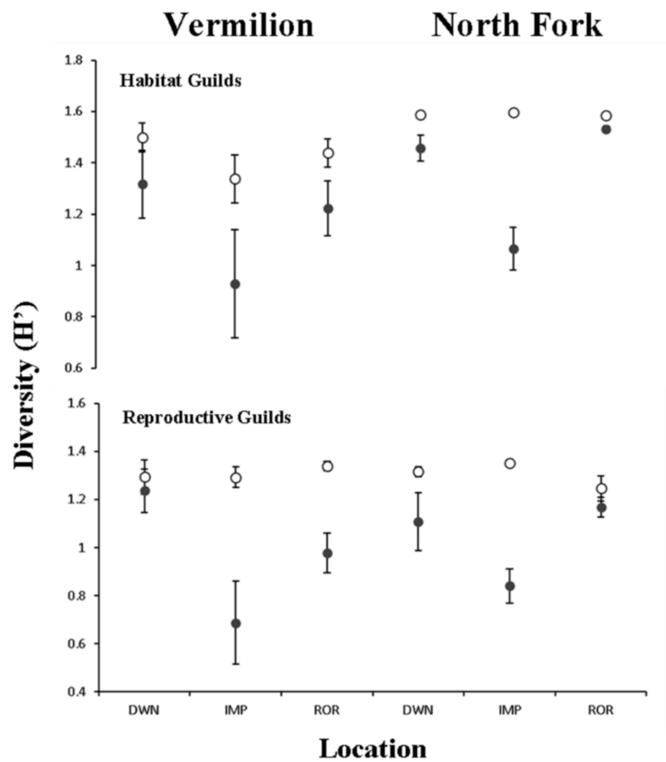
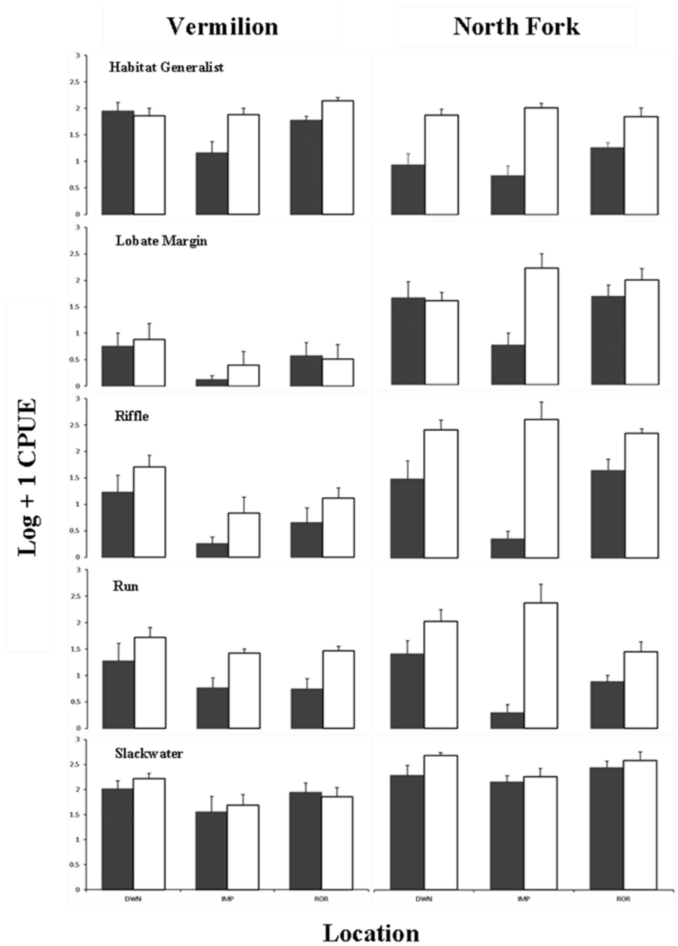
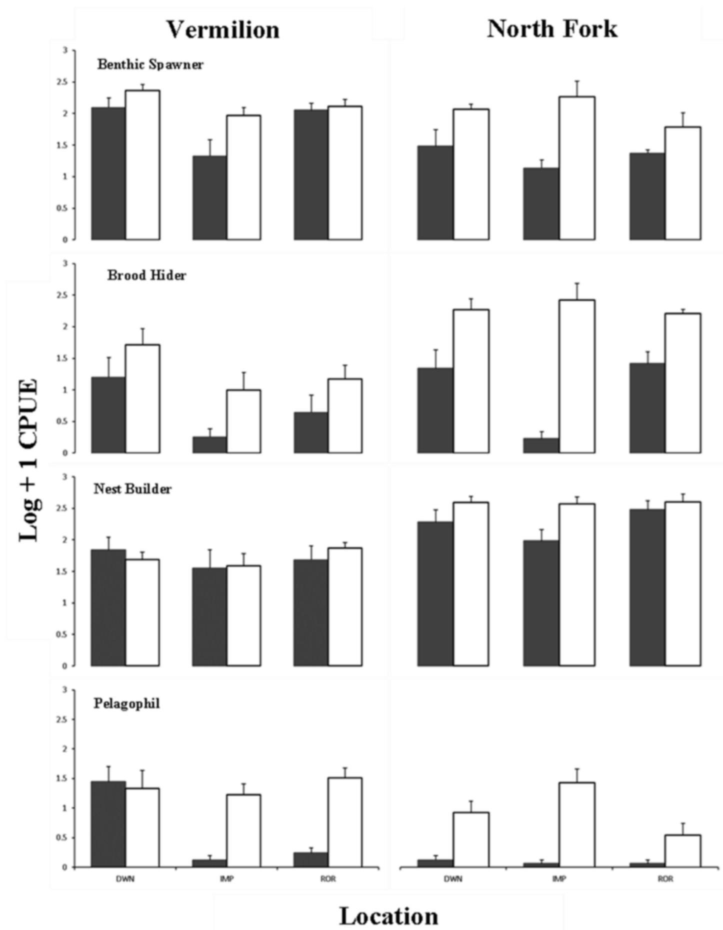
IMP
ROR
DWN
IMP
ROR
Location


Vermilion
North Fork
Log CPUE
3.5
3
2.5
2
1.5
1
DWN
IMP
ROR
DWN
IMP
ROR
Location


Habitat Guilds
Reproductive Guilds
Vermilion
North Fork
Pre-Removal
Post-Removal
DWN
IMP
ROR
Slackwater
Lobate Margin
QHEI
Riffle
Run
IBI
Habitat Generalist
Nest Builder
Bearer
Brood Hider
Benthic Spawner
Pelagophil
NMDS2
NMDS1


Vermilion
North Fork
Habitat Guilds
Reproductive Guilds
Diversity (H')
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
DWN
IMP
ROR
DWN
IMP
ROR
Location


Vermilion
North Fork
Habitat Generalist
Lobate Margin
Riffle
Run
Slackwater
Log + 1 CPUE
Location
DWN
IMP
ROR


Vermilion
North Fork
Benthic Spawner
Brood Hider
Nest Builder
Pelagophil
Log + 1 CPUE
DWN
IMP
ROR
Location