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# Short-term consequences of lowhead dam removal for fish assemblages in an urban river system

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With 7 figures and 1 table

**Abstract:** Lowhead or run-of-river dams, which can have significant impacts on river ecosystems, are common on rivers around the world. Although lowhead dam removal is becoming an increasingly viable component of river restoration projects, the quantitative effects of lowhead dam removal on river ecosystems are not well described. In this study, we investigated the short-term (< 2 years) effects of two lowhead dam removals on fish assemblage diversity and structure in the Scioto and Olentangy Rivers of urban Columbus, Ohio (USA). Non-metric multidimensional scaling (NMS) and analysis of similarities (ANOSIM) revealed that upstream assemblage composition shifted significantly from before to after dam removal (ANOSIM; $R = 0.714$, $p = 0.001$). Likewise, assemblage shifts were significant between years 1 and 2 at Olentangy River reaches both upstream and downstream of dam removal (ANOSIM; $R = 0.136$, $p = 0.019$). Shifts in fish diversity metrics were accompanied by changes in relative abundances of taxa within feeding guilds. For example, reductions in species richness and diversity at upstream reaches were accompanied by the loss of large-bodied omnivorous species. In the second year following dam removal, a significant increase in assemblage diversity at an upstream restored reach (including colonization by sensitive *Etheostoma* species) was accompanied by an increase in insectivores and a reduction of larger-bodied omnivores and carnivores. Overall, our results suggest that dam removal may act as a pulse disturbance with quantitative short-term impacts on fish assemblages. Fish responses to dam removal likely operate along a temporal trajectory wherein short-term responses will be critical in shaping longer-term responses.

**Keywords:** disturbance, fish assemblage diversity and composition, lowhead dam removal, river restoration, urbanization

## Introduction

Over half of the large rivers in the world are affected by dams (Nilsson et al. 2005), which are widely known to have substantial impacts on fluvial systems (Ligon et al. 1995; Doyle et al. 2005; Nilsson et al. 2005; Poff et al. 2007). For fish, the effects of dams are well established (Bednarek 2001; Bunn & Arthington 2002; Dudley & Platania 2007) and linked to altered flow regimes (Winston et al. 1991; Gehrke et al. 2002; Helms et al. 2011) that can force shifts from predominantly lotic-adapted (flowing) to lentic-adapted (still water) species (Power et al. 1996). Furthermore, changes in water temperature resulting from impoundments can prompt a suite of responses including shifts in fish distribution and behavior, changes in metabolic rates, and altered community composition (reviewed in Helms et al. 2011). Reduced longitudinal connectivity in streams and rivers can lead to isolated fish populations

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(Dudley & Platania 2007; Roberts et al. 2013) and reductions in genetic diversity (Morita & Yokota 2002; Tsuboi et al. 2010).

Although dams vary considerably in size relative to both height and width, criteria used to classify dams by size are highly inconsistent (reviewed in Poff & Hart 2002). Operational characteristics relative to reservoir storage capacity are also used to categorize dams as either storage or run-of-river (US Bureau of Reclamation 2013). For the purposes of our study, we defined lowhead dams as run-of-river dams with a hydraulic head ≤ 7.5 m (Stanly et al. 2002), with reference to "large" dams as storage dams > ~7.5 m in height. Within this framework, the majority of attention to date has been directed towards large dams (Hill et al. 1994; Shuman 1995; Pess et al. 2008). However, lowhead dams are widespread; according to the National Inventory of Dams (NID) by the United States Army Corps of Engineers (2013), 43,029 dams of the 87,035 surveyed in the continental United States are < 7.62 m in height (although note that the NID does not include dams < 7.62 m that are of low or no significant hazard to humans).

Lowhead dams can also have pronounced impacts on fish assemblages (Santucci et al. 2005; Helms et al. 2011; Gardner et al. 2013). Lowhead dams fragment river systems and impede or prevent fish dispersal and migration into critical habitats (Porto et al. 1999; Katano et al. 2006; McLaughlin et al. 2006). Several studies have found that impounded river segments have lower species richness than downstream sections (Kanehl et al. 1997; Santucci et al. 2005; Helms et al. 2011). In addition to the physical barriers imposed by dams, declines in richness and abundance associated with lowhead dams may also be related to greater sediment storage, increased habitat homogenization, and loss of food resources (Bunn & Arthington 2002; Gardner et al. 2013; Van Looy et al. 2014). The relative impact of lowhead dams is likely mediated by landscape features (e.g., land use and land cover, riparian buffers), variability in natural processes (e.g., flow regime, biogeochemical cycling, geology), and management practices (e.g., controlled water releases) (reviewed in Poff & Hart 2002; Cumming 2004), underscoring the importance of the broader environmental context.

Given that dams represent such highly influential structures, their removal might be expected to represent an ecologically meaningful disturbance (*sensu* Resh et al. 1988) with profound consequences for fish assemblages (Bednarek 2001; Gregory et al. 2002; Doyle et al. 2005). However, the potential impacts of dam removal – and particularly of lowhead dam removal – remain poorly resolved. The effects of lowhead dams, and by extension their removal, are unlikely to be comparable with larger dams (Hart et al. 2002; reviewed in Poff & Hart 2002). To date, evidence suggests that fish species richness and diversity tends to increase upstream of previous dam locations (Catalano et al. 2007; Burroughs et al. 2010; Gardner et al. 2013), returning to lotic-type communities (Bushaw-Newton et al. 2002; Maloney et al. 2008). Conversely, downstream assemblages have been shown to decline in species richness, abundance, and diversity shortly following dam removal (Catalano et al. 2007; Gardner et al. 2013).

Ecosystem responses to dam removal may range from immediate (i.e., several months) to several decades (Hart et al. 2002; Doyle et al. 2003a; Doyle et al. 2005). Whereas some studies have shown shifts in fish assemblages only a year after dam removal (Burdick & Hightower 2006; Catalano et al. 2007; Fjeldstad et al. 2012; Gardner et al. 2013), others have demonstrated that quantitative changes occurred only after several years (Doyle et al. 2005; Stanley et al. 2007; Maloney et al. 2008). For example, Kanehl et al. (1997) documented changes in fish assemblages following removal of a ~6-m high Wisconsin dam, including a decrease in the relative abundance of common carp (*Cyprinus carpio*), an increase in the relative abundance of smallmouth bass (*Micropterus dolomieu*), and increased habitat condition and Index of Biotic Integrity scores in the previously impounded area. For some characteristics, the impact of dam removal was almost immediate (e.g., common carp decrease), whereas for others (e.g., smallmouth bass increase) there appeared to be a longer time lag following dam removal (Kanehl et al. 1997).

In the past several decades, nearly 500 dams of various sizes and functions have been removed in the United States and the number continues to grow (Bushaw-Newton et al. 2002; Gregory et al. 2002; reviewed in Poff & Hart 2002; reviewed in Stanley & Doyle 2003). Thus, understanding and predicting the responses of fish assemblages to dam removal is critical for both conservation and restoration outcomes (Pess et al. 2008). Here, we investigated the short-term (< 2 years) effects of lowhead dam removal and the role of associated restoration activities on fish assemblage diversity and composition in urban Columbus, Ohio (USA). To do this, we sampled fish assemblages before and after the removal of two lowhead dams ("5th Avenue Dam", 2.5 m in height; "Main Street Dam", 4.1 m in height) in the Scioto River system and compared fish assemblage characteristics over space (upstream and downstream of previous dams) and time (before removal, +1 year and +2 years following dam removal). Because active channel and riparian restoration activities were associated with the 5th Avenue dam removal, we also compared fish assemblage responses in restored versus adjacent non-restored river reaches.

We predicted that dam removal acts as an ecologically-significant pulse disturbance leading to short-term shifts in fish assemblages. More specifically, we hypothesized that following dam removal, upstream fish assemblages would respond to increased flow variability and greater habitat heterogeneity via increases in both species and functional (as measured by feeding guilds) diversity and that these shifts would increase in magnitude from year 1 to year 2 following dam removal. Conversely, we hypothesized that erosion of impounded sediment, leading to transport and deposition of sediment downstream, would prompt rapid but short-lived declines in species richness and a homogenization of feeding guilds following dam removal.

## Methods

### Study system and design

We surveyed seven stream reaches in the Olentangy and Scioto Rivers in Columbus, Ohio using a Before-After Control-Impact design (Stewart-Oaten et al. 1986; Kibler

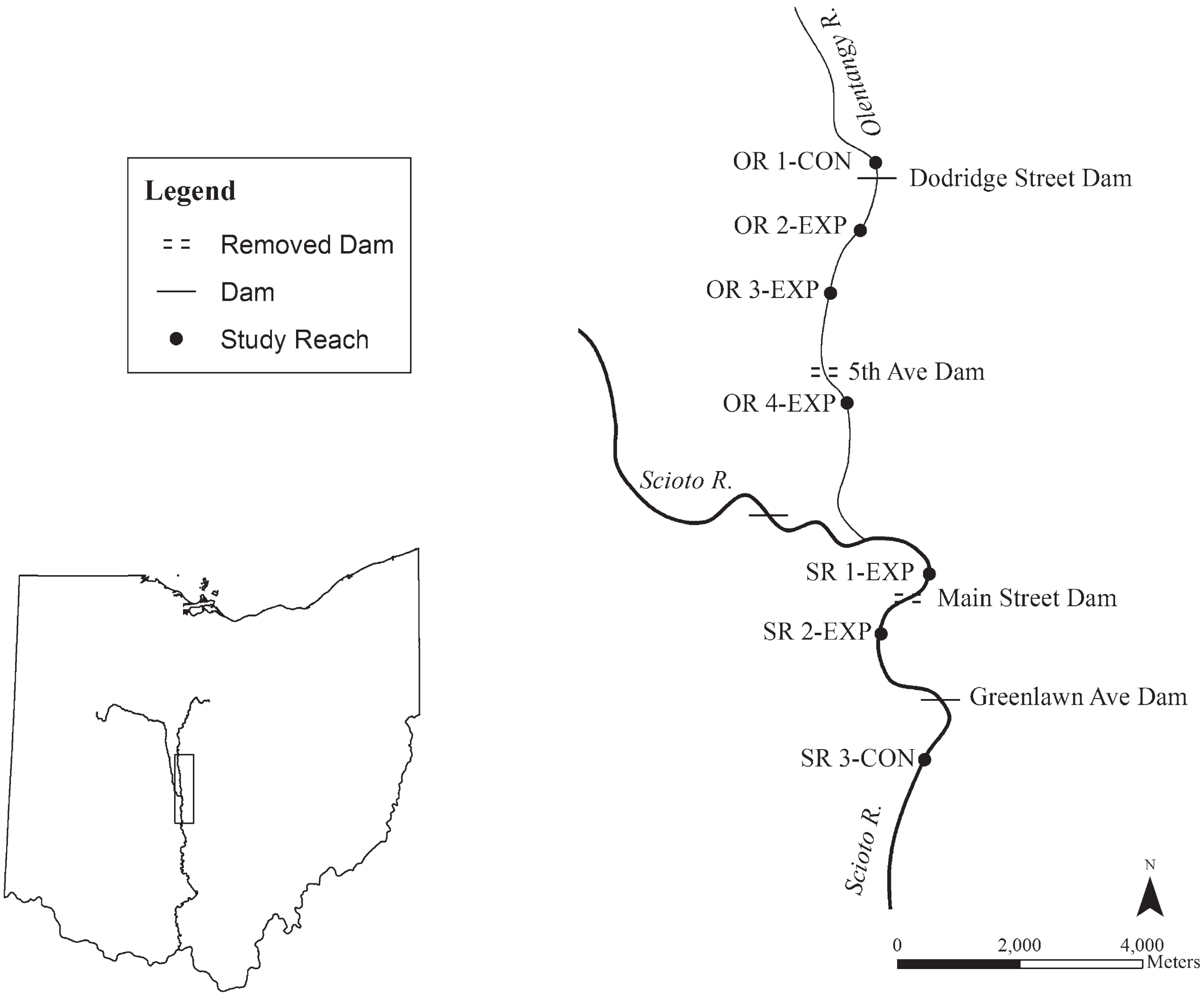


**Fig. 1.** The Olentangy and Scioto River study area in central Ohio (Columbus, OH, USA). Olentangy River reaches (OR 1-4) were located upstream and downstream of the 5th Avenue Dam that was removed in August 2012. Scioto reaches (SR 1-3) were located upstream and downstream of the Main Street Dam, which was removed in November 2013. The labels "CON" and "EXP" indicate control and experimental reaches, respectively. OR1 and SR3 represent upstream and downstream control reaches, respectively. OR2 and OR3 represent the unmanipulated and actively restored upstream Olentangy experimental reaches, respectively. OR4 represents the downstream Olentangy experimental reach. SR1 and SR2 represent upstream and downstream Scioto experimental reaches, respectively. All dams (current and removed) are/were lowhead, run-of-river dams (≤ ~7.5 m in height).

et al. 2011). Our 500-m study reaches were distributed both upstream and downstream of lowhead dams scheduled for removal in 2012 (5th Avenue Dam, Olentangy River) and 2013 (Main Street Dam, Scioto River) (Fig. 1). The Olentangy River is a 5th-order, 156-km tributary of the Scioto River. The Olentangy River study reaches were located upstream and downstream of the 5th Avenue Dam, built in 1935 to provide cooling water for a now inactive power plant of The Ohio State University. Removal of the 5th Avenue Dam and subsequent active restoration efforts were aimed at improving water quality and aquatic habitat (US Army Corps of Engineers 2004). In addition to the dam removal, restoration efforts included channel restoration at sections of a 2.6-rkm river segment, including reshaping the river channel, redeveloping and reconnecting floodplain wetlands, and planting riparian vegetation (see Ohio EPA 2011 for additional details) upstream of the previous dam. Restoration only included a segment of the previous impoundment, leaving an unrestored upstream reach (OR2, Fig. 1). Restoration activities occurred throughout the entire restored upstream reach (OR3, Fig. 1). Our upstream control reach, OR1 (Fig. 1), was located above an intact lowhead dam of comparable age and height to the 5th Avenue Dam.

The Scioto River is a 372 km, 6th-order tributary of the Ohio River. Study reaches on the Scioto River were located upstream and downstream of the Main Street Dam in downtown Columbus, which was constructed in the late 1800s largely for aesthetic purposes and removed in November 2013 to improve water quality, habitat, and increase riverfront access. This dam removal did not include in-stream restoration, although newly exposed riverbanks were partly reestablished and recontoured from substrate that remained after dam removal. Our downstream control reach, SR3, was located downstream of the Main Street Dam and separated from SR2 by the lowhead Greenlawn Avenue Dam (Fig. 1). We assigned study reaches to several treatments (e.g., upstream/downstream of dams, restored/unrestored sections, before/after) to assess the impacts of dam removal and subsequent restoration activities on fish assemblage composition. For clarity, control reaches are designated as “upstream control” and “downstream control”; all others are designated as “experimental reaches” (Fig. 1).

### Fish surveys

All fish surveys were conducted between 2011–2014 during the stable, baseflow period of late summer-early autumn. Prior to dam removal, OR1 and SR3 (upstream and downstream controls, respectively) as well as experimental reaches OR3, SR1, and SR2 were sampled. All reaches were sampled one year following dam removal; additionally, all Olentangy reaches were sampled two years following dam removal. We stratified each reach into bottom, middle, and top sections and then within each of these sections by right bank, mid-channel, and left bank transects (running longitudinally, upstream to downstream within each section). Depending on the physical characteristics (e.g., depth, conductivity) of the study reach, we electrofished each of the nine transects using a Smith-Root® LR-24 backpack electrofisher, 2.5 GPP Smith-Root® shoreline electrofisher, and/or a 5 GPP Smith-Root® (Smith-Root, Vancouver, Washington) boat unit. For each reach, sampling effort was based on a pre-dam removal effort of 600 s per section (total of 5,400 s per reach). Consistent with other dam-removal studies, sampling effort was then adjusted according to changes in habitat volume and complexity following dam removal (Port et al. 2006; Catalano et al. 2007; Maloney et al. 2008). All fish were held in aerated live-wells and released back into the river following identification and enumeration. Feeding guilds were assigned to each species based on Angermeier and Karr’s Index of Biotic Integrity (Angermeier & Karr 1986).

### Numerical and statistical analysis

We calculated species richness (*S*), Shannon-Weiner Diversity Index (*H*’), and species evenness (*E*) for each transect (i.e., bottom, middle, and top) along the entire study reach, which were then averaged to generate reach-wide mean values. The Shannon-Weiner Index is an informational index in which both a greater number of species and a more even distribution contribute to greater *H*’.

$$H' = \sum_{i=1}^{s} p_i ln p_i \tag{1}$$

where $p_i$ is the proportion of the total sample represented by species *i*.

Species evenness (*E)* quantifies the relative abundances of species within the assemblage and ranges from 0 to 1 where communities with an equitability number closer to 1 represent greater evenness.

$$E = \frac{H'}{H'_{\max}} \tag{2}$$

where $H'_{\max}$ is the natural log of species richness (*S*).

We performed two-sample *t*-tests using JMP 11.0 (SAS Institute, Cary, North Carolina) to test for potential differences in fish assemblage *S*, *H*’, and *E* before and after dam removal, +1 and +2 years after dam removal, upstream and downstream of dam removal, and between

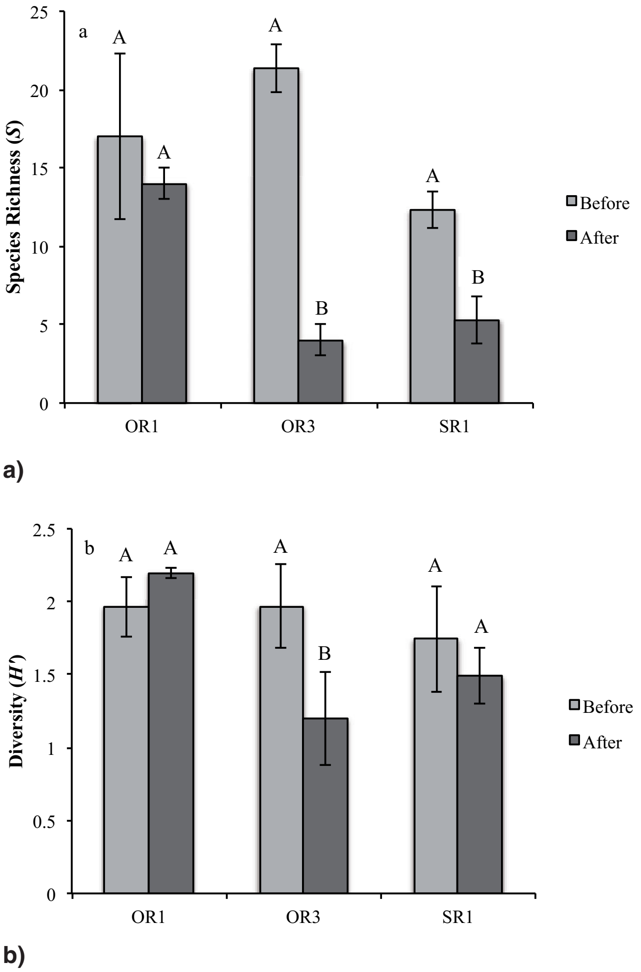


**Fig. 2.** Upstream fish assemblage (a) species richness (*S*) and (b) diversity (*H'*) before and one year following dam removal at OR1 (upstream control), OR3 (upstream experimental), and SR1 (upstream experimental). Significant differences based on *t*-tests are indicated by different letters ($p < 0.05$). Error bars represent ±1 standard error (SE) from the mean.

the upstream restored and unrestored Olentangy River experimental reaches.

We used non-metric multidimensional scaling (NMS) followed by analysis of similarities (ANOSIM) to test for differences in fish assemblage composition (1) between control and experimental reaches upstream from dams (e.g., OR1, OR3, SR1), (2) before and after dam removal and, (3) between Olentangy River control and experimental reaches (e.g., OR1, OR2, OR3, OR4) across successive years following dam removal. We conducted NMS with relative abundance data of fish species using Sorenson's (Bray-Curtis) distance and 500 randomizations. We selected a two-dimensional solution with a stability criterion of 0.00001. The NMS arrived at a two-dimensional solution after 25 (Before-After NMS) and 23 (Year1-Year2 After NMS) iterations. In our case, NMS was used to graphically display relationships between treatments in multidimensional space. The relative position of treatments in NMS plots represented the underlying dissimilarities in fish assemblages among those treatments. We displayed ordination results using joint plots showing relationships among species abundances relative to treatments. All species exhibiting Pearson's $r > 0.25$ were displayed in joint plots; although those more strongly correlated (Pearson's $r > 0.5$) received greater consideration in the interpretation of the plots. ANOSIM uses Bray-Curtis dissimilarities to test for differences among groups based on the average rank dissimilarities within groups compared to the average rank dissimilarities between groups (Clarke 1993). PC-ORD 5 (MjM Software Design, Gleneden Beach, OR) was used for NMS (McCune et al. 2002) and the package "vegan" (Oksanen et al. 2013) within R (R Core Team 2014) for ANOSIM tests.

## Results

### Fish assemblages before and after dam removal

Fifty-seven fish species were surveyed across the sampling years, 49 in the Olentangy River and 43 in the Scioto River. Prior to dam removal, species richness was highest at OR3 ($\bar{x} = 21.3$, SD = 1.5) and SR2 ($\bar{x} = 17.3$, SD = 0.6). *H'* was highest at the downstream Scioto reaches (SR2 and SR3; note that SR3 represents the downstream control) and lowest at SR1. *E* was also highest at the downstream Scioto reaches (Table 1).

One year following dam removal, species richness had significantly declined in both the Olentangy (OR3; $t = -19.65$, $df = 2$, $p = 0.003$) and the Scioto (SR1; $t = -12.12$, $df = 2$, $p = 0.007$) upstream experimental reaches, but not in the upstream control reach (OR1: $p > 0.05$) (Fig. 2a). Likewise, although *H'* was invariant in the upstream control reach ($p > 0.05$), it declined appreciably following dam removal for upstream Olentangy and downstream Scioto experimental reaches (OR3: $t = -9.95$, $df = 2$, $p = 0.010$; SR2: $t = -14.53$, $df = 2$, $p = 0.005$). Species evenness at OR3 was greater following dam removal than before dam removal ($t = 4.59$, $df = 2$, $p = 0.044$); *E* did not change significantly at the upstream Scioto experimental reach (SR1; $p > 0.05$; data not shown).

NMS ordination for before-after dam removal in upstream treatments resulted in a two-dimensional solution (stress = 4.394, $p = 0.065$). The first axis accounted for 13.9% of variation in fish assemblages across treatments; whereas the second axis accounted for 50.1% of this variation. Before dam removal, fish assemblage composition

**Table 1.** Fish assemblage summary statistics for species richness (*S*), Shannon-Weiner Diversity Index (*H'*), and species evenness (*E*) for control and experimental reaches sampled before and one year following dam removal on the Olentangy and Scioto Rivers, Ohio, USA.

| | **Before** | | | | | **Year 1** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Min** | **Max** | **Median** | **Mean** | **SD** | **Min** | **Max** | **Medain** | **Mean** | **SD** |
| ***Upstream Control (OR1)*** | | | | | | | | | | |
| *S* | 11 | 21 | 19 | 17 | 5.3 | 13.0 | 15.0 | 14.0 | 14.0 | 1.0 |
| *H'* | 1.733 | 2.125 | 2.044 | 1.967 | 0.207 | 2.169 | 2.24 | 2.189 | 2.199 | 0.037 |
| *E* | 0.694 | 0.723 | 0.698 | 0.705 | 0.016 | 0.732 | 0.830 | 0.801 | 0.788 | 0.050 |
| ***Olentangy Upstream Experimental – Unrestored (OR2)*** | | | | | | | | | | |
| *S* | | Data | not | available | | 5.0 | 10.0 | 9.0 | 8.0 | 2.6 |
| *H'* | | | | | | 1.438 | 1.846 | 1.605 | 1.63 | 0.205 |
| *E* | | | | | | 0.731 | 0.893 | 0.802 | 0.809 | 0.081 |
| ***Olentangy Upstream Experimental – Restored (OR3)*** | | | | | | | | | | |
| *S* | 20.0 | 23.0 | 21.0 | 21.3 | 1.5 | 3.0 | 5.0 | 4.0 | 4.0 | 1.0 |
| *H'* | 1.659 | 2.226 | 2.019 | 1.968 | 0.287 | 0.937 | 1.561 | 1.099 | 1.199 | 0.324 |
| *E* | 0.529 | 0.731 | 0.674 | 0.645 | 0.104 | 0.676 | 1.000 | 0.970 | 0.882 | 0.179 |
| ***Olentangy Downstream Experimental (OR4)*** | | | | | | | | | | |
| *S* | | Data | not | available | | 4.0 | 7.0 | 5.0 | 5.3 | 1.5 |
| *H'* | | | | | | 1.072 | 1.691 | 1.089 | 1.284 | 0.353 |
| *E* | | | | | | 0.666 | 0.869 | 0.786 | 0.775 | 0.102 |
| ***Scioto Upstream Experimental (SR1)*** | | | | | | | | | | |
| *S* | 11.0 | 13.0 | 13.0 | 12.3 | 1.2 | 4.0 | 7.0 | 5.0 | 5.3 | 1.5 |
| *H* | 1.377 | 2.104 | 1.757 | 1.746 | 0.364 | 1.277 | 1.639 | 1.561 | 1.492 | 0.191 |
| *E* | 0.574 | 0.820 | 0.685 | 0.693 | 0.123 | 0.842 | 0.970 | 0.921 | 0.911 | 0.065 |
| ***Scioto Downstream Experimental (SR2)*** | | | | | | | | | | |
| *S* | 17.0 | 18.0 | 17.0 | 17.3 | 0.6 | 8.0 | 12.0 | 10.0 | 10.0 | 2.0 |
| *H'* | 2.496 | 2.701 | 2.584 | 2.594 | 0.103 | 1.245 | 1.596 | 1.523 | 1.455 | 0.185 |
| *E* | 0.881 | 0.934 | 0.912 | 0.909 | 0.027 | 0.541 | 0.768 | 0.613 | 0.641 | 0.116 |
| ***Scioto Downstream Control (SR3)*** | | | | | | | | | | |
| *S* | 11.0 | 20.0 | 16.0 | 15.7 | 4.5 | 14.0 | 16.0 | 15.0 | 15.0 | 1.0 |
| *H'* | 2.008 | 2.614 | 2.54 | 2.387 | 0.331 | 1.777 | 2.016 | 1.838 | 1.877 | 0.124 |
| *E* | 0.837 | 0.916 | 0.873 | 0.875 | 0.04 | 0.641 | 0.764 | 0.679 | 0.695 | 0.063 |

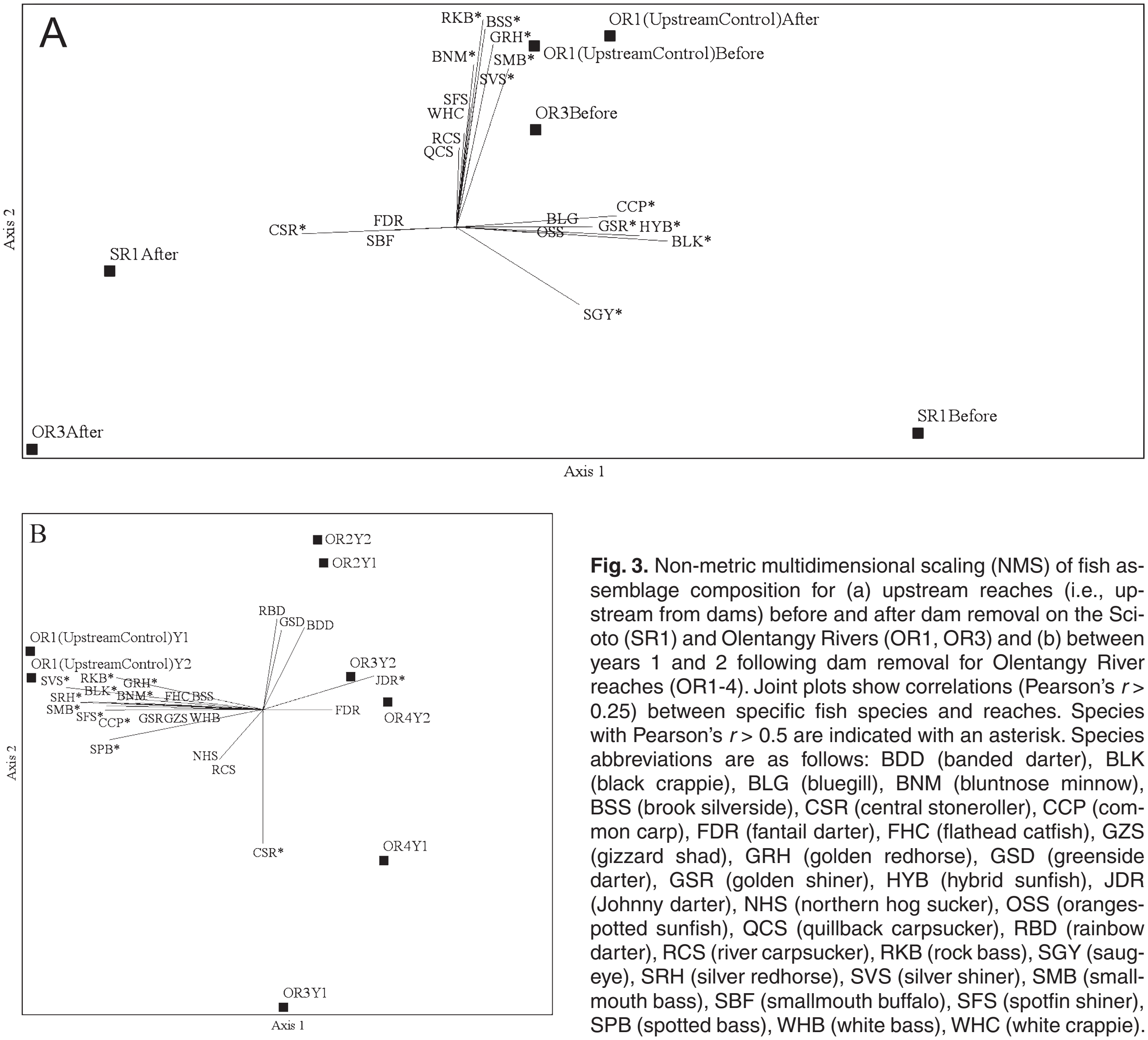


**Fig. 3.** Non-metric multidimensional scaling (NMS) of fish assemblage composition for (a) upstream reaches (i.e., upstream from dams) before and after dam removal on the Scioto (SR1) and Olentangy Rivers (OR1, OR3) and (b) between years 1 and 2 following dam removal for Olentangy River reaches (OR1-4). Joint plots show correlations (Pearson's $r > 0.25$) between specific fish species and reaches. Species with Pearson's $r > 0.5$ are indicated with an asterisk. Species abbreviations are as follows: BDD (banded darter), BLK (black crappie), BLG (bluegill), BNM (bluntnose minnow), BSS (brook silverside), CSR (central stoneroller), CCP (common carp), FDR (fantail darter), FHC (flathead catfish), GZS (gizzard shad), GRH (golden redhorse), GSD (greenside darter), GSR (golden shiner), HYB (hybrid sunfish), JDR (Johnny darter), NHS (northern hog sucker), OSS (orangespotted sunfish), QCS (quillback carpsucker), RBD (rainbow darter), RCS (river carpsucker), RKB (rock bass), SGY (saugeye), SRH (silver redhorse), SVS (silver shiner), SMB (smallmouth bass), SBF (smallmouth buffalo), SFS (spotfin shiner), SPB (spotted bass), WHB (white bass), WHC (white crappie).

in upstream reaches consisted of higher relative abundances of common carp, smallmouth and rock bass (*Ambloplites rupestris*), golden redhorse (*Moxostoma erythrurum*), brook silverside (*Lebidesthes sicculus*), silver (*Notropis photogenis*) and golden (*Notemigonus crysoleucas*) shiners, bluntnose minnow (*Pimephales notatus*), black crappie (*Pomoxis nigromaculatus*) and hybrid sunfish (*Lepomis* spp.) (Fig. 3a). Saugeye (*Stizostedion vitreum x S. canadense*) were also more prevalent in SR1 prior to dam removal. Following dam removal, the fish assemblage at the upstream control reach (OR1) changed little. However, both SR1 and OR3 fish assemblages changed significantly one year after dam removal (ANOSIM; $R = 0.714$, $p = 0.001$), largely driven by both reduced abundances of the common species surveyed in predam removal impoundments as well as the appearance and/or increased abundance of species such as central stoneroller (*Campostoma anomalum*), fantail darter (*Etheostoma flabellare*), and smallmouth buffalo (*Ictiobus bubalus*).

Shifts in fish assemblage composition at the upstream Olentangy and Scioto reaches were accompanied by shifts in presence and relative abundance of taxa in different feeding guilds (Fig. 4). Prior to dam removal, omnivorous and insectivorous species dominated the assemblages (Figs 4a, c, e). Following dam removal, the relative abun-

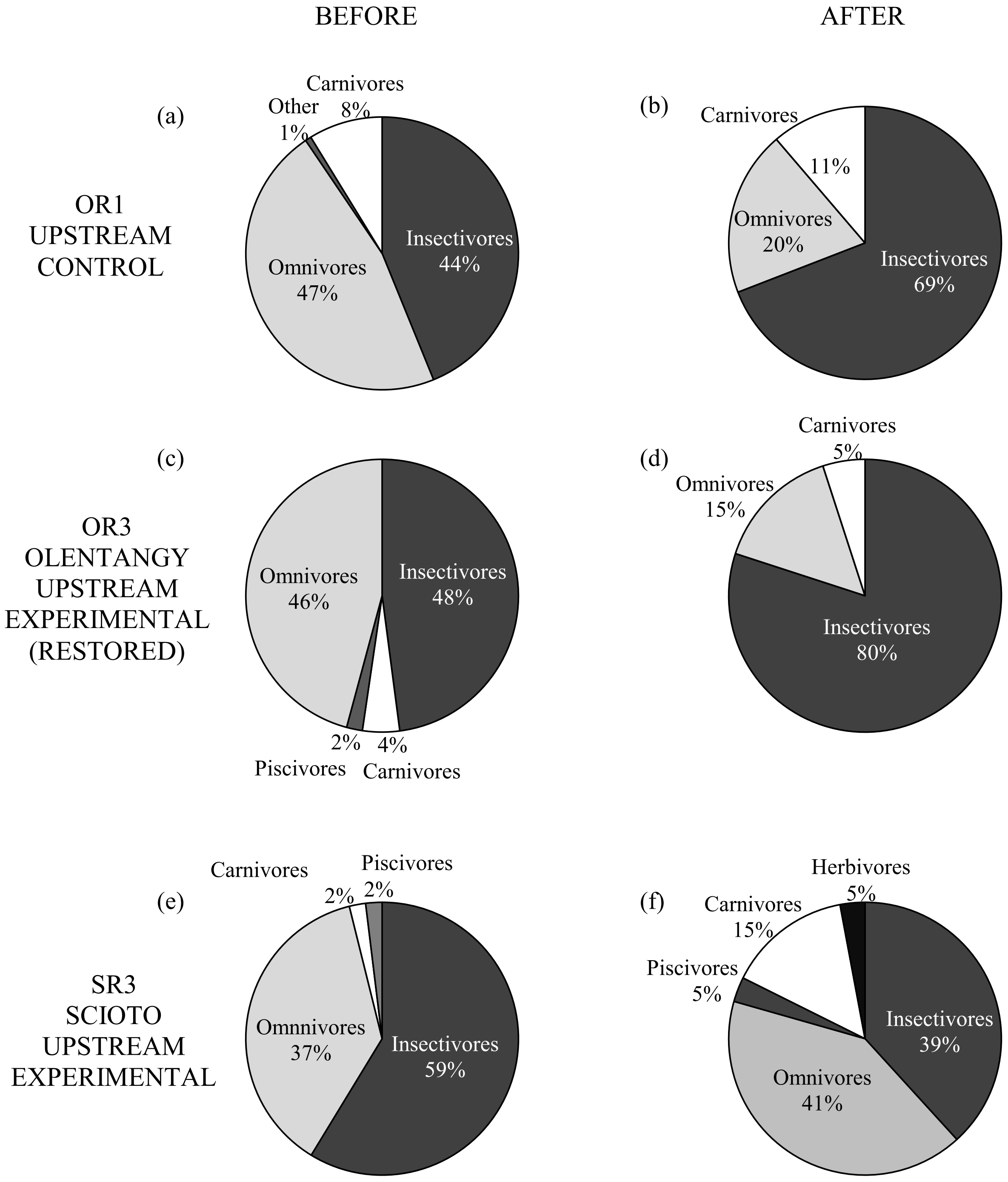


**Fig. 4.** Proportion of fish assemblage by representative feeding guilds at the upstream Olentangy and Scioto River reaches: (a) OR1 before, (b) OR1 after, (c) OR3 before, (d) OR3 after, (e) SR1 before, and (f) SR1 after.

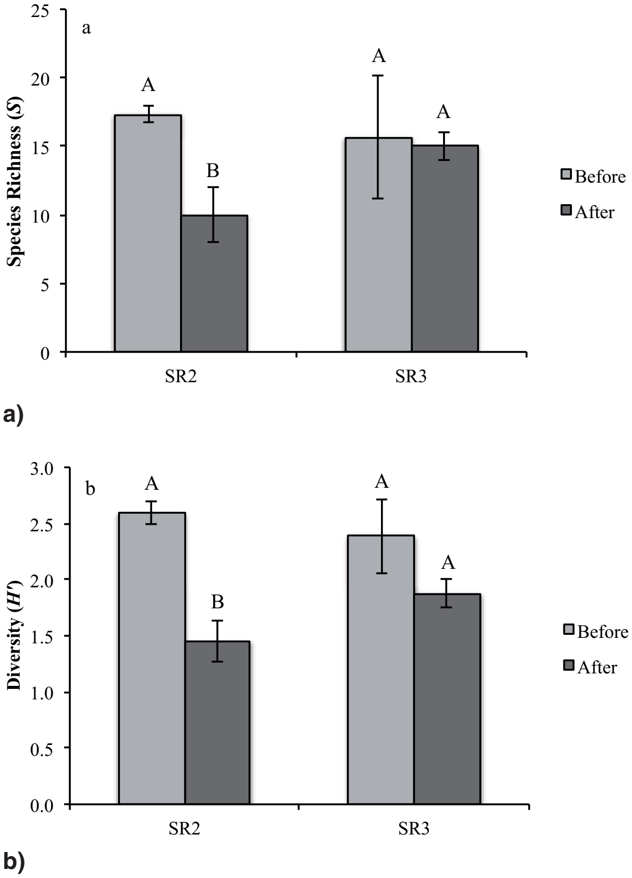


**Fig. 5.** Downstream fish assemblage (a) species richness (*S*) and (b) diversity (*H'*) before and one year following dam removal at SR2 (downstream experimental) and SR3 (downstream control). Significant differences based on *t*-tests are indicated by different letters ($p < 0.05$). Error bars represent ±1 standard error (SE) from the mean.

dance of omnivores declined at OR3 with a corresponding 32% increase in the relative abundance of insectivores (Fig. 4d). Conversely, the proportion of insectivores decreased by 20% in the upstream Scioto reach (SR1; Fig. 4f). Note that the proportion of insectivores increased by 25% in the upstream control reach on the Olentangy River (Fig. 4).

Given logistical constraints (outlined in the Methods), our results relative to downstream consequences of dam removal were limited to one experimental and one control reach on the Scioto River. *S* and *H'* (Fig. 5) decreased significantly at the downstream experimental reach (SR2: *S* – $t = -8.32$, $df = 2$, $p = 0.014$; *H'* – $t = -14.53$, $df = 2$, $p = 0.005$), but not at the downstream control reach (SR3: $p > 0.05$ for both *S* and *H'*). *E* did not decline at SR2 ($p > 0.05$), although *E* was significantly lower at the downstream control reach (SR3: $t = -12.59$, $df = 2$, $p = 0.006$; data not shown). Following removal of the Main Street Dam on the Scioto River, *E* between the upstream and downstream Scioto fish assemblages was significantly different ($t = -4.44$, $df = 2$; $p = 0.047$), although *H'* and *S* did not differ significantly between these same reaches ($p > 0.05$).

## Short-term fish assemblage shifts following dam removal

For the Olentangy River, we observed significant changes in fish assemblages between the first and second years following dam removal. Species richness increased 2.5 times at OR3 ($t = 6.00$, $df = 2$, $p = 0.027$) and showed an in-

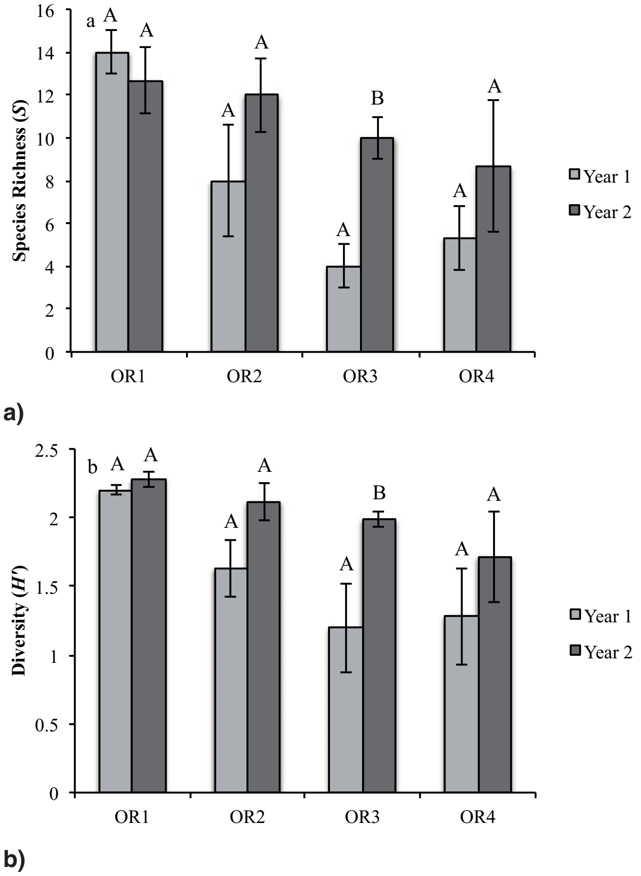
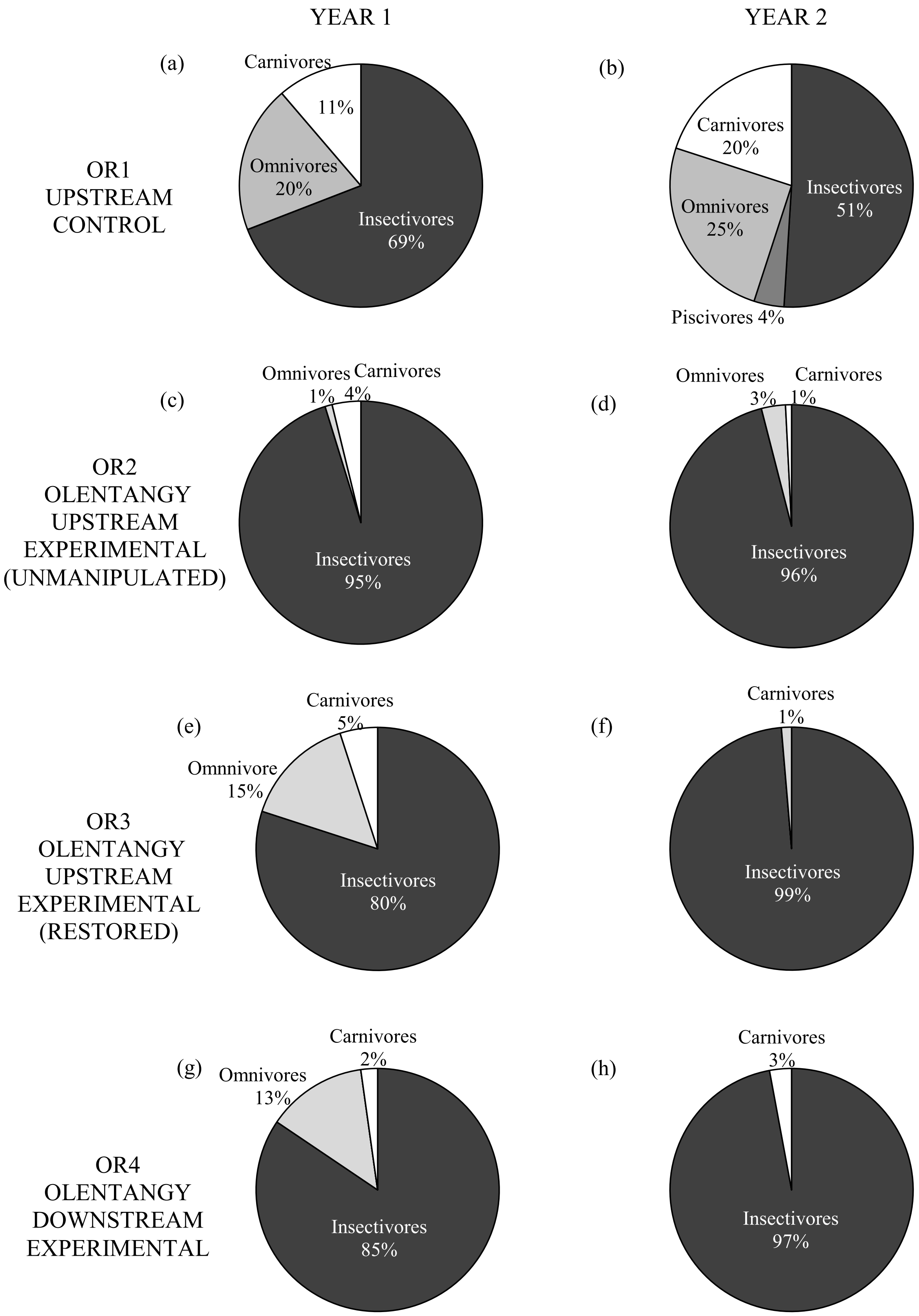


**Fig. 6.** Fish assemblage (a) species richness and (b) diversity (*H'*) in years 1 and 2 following dam removal of the Olentangy River study reaches. OR1 is the upstream control reach; OR2 is the upstream, unmanipulated experimental reach; OR3 is the upstream, restored experimental reach; and OR 4 is the downstream experimental reach. Significant differences based on *t*-tests are indicated by different letters ($p < 0.05$). Error bars represent ±1 standard error (SE) from the mean.


YEAR 1
YEAR 2
(a)
Carnivores
11%
Omnivores
20%
Insectivores
69%
(b)
Carnivores
20%
Insectivores
51%
Omnivores
25%
Piscivores 4%
OR1
UPSTREAM
CONTROL
(c)
Omnivores
1%
Carnivores
4%
Insectivores
95%
(d)
Omnivores
3%
Carnivores
1%
Insectivores
96%
OR2
OLENTANGY
UPSTREAM
EXPERIMENTAL
(UNMANIPULATED)
(e)
Carnivores
5%
Omnnivore
15%
Insectivores
80%
(f)
Carnivores
1%
Insectivores
99%
OR3
OLENTANGY
UPSTREAM
EXPERIMENTAL
(RESTORED)
(g)
Carnivores
2%
Omnivores
13%
Insectivores
85%
(h)
Carnivores
3%
Insectivores
97%
OR4
OLENTANGY
DOWNSTREAM
EXPERIMENTAL

creasing trend at the Olentangy downstream experimental reach (OR4: $t = 3.78$, $df = 2$, $p = 0.063$) [Fig. 6a; note no difference in upstream control reach (OR1) between years 1 and 2 ($p > 0.05$); Table 1]. *H*' increased significantly at the upstream restored (OR3: $t = 4.76$, $df = 2$, $p = 0.042$) and downstream experimental (OR4: $t = 6.12$, $df = 2$, $p = 0.026$) reaches (Fig. 6b). Species richness and *H'* at OR3 were lower than at the unrestored OR2 (*S*: $t = -5.29$, $df = 2$, $p = 0.034$; *H*': $t = -5.912$, $df = 2$, $p = 0.027$) in spite of considerable in-channel and floodplain restoration activities beginning in the summer of 2013. However, both reaches exhibited increases in species richness and *H'* in the second year following dam removal so that neither *S* nor *H*' was different between reaches in year 2 ($p > 0.05$; Fig. 6). *E* was not significantly different at the upstream restored and downstream experimental reaches between years 1 and 2. However, *E* increased significantly in the upstream control (OR1: $t = 21.75$, $p = 0.0021$, $df = 2$) and upstream unrestored (OR2: $t = 8.31$, $df = 2$, $p = 0.014$) reaches between years 1 and 2. *E* did not differ between the upstream restored and unrestored experimental reaches immediately after or in the second year following dam removal ($p > 0.05$).

NMS ordination for year 1 to year 2 after dam removal at the Olentangy River reaches resulted in a two-dimensional solution (stress = 3.340, $p = 0.032$). The first axis accounted for 52.2% of variation in fish assemblages across treatments; whereas the second axis accounted for 37.1% of this variation. Assemblage composition at the upstream control reach (OR1) and the upstream unrestored experimental reach (OR2) changed little between the first and second years following dam removal (Fig. 3b). Assemblage composition changed more substantially from year 1 to year 2 at the upstream restoration (OR3) and the downstream (OR4) experimental reaches (ANOSIM; $R = 0.136$, $p = 0.019$). Following dam removal and subsequent restoration activities, assemblages at OR3 and OR4 shifted as a number of darter species [e.g., banded darter (*Etheostoma zonale*), Johnny darter (*Etheostoma nigrum*), rainbow darter (*Etheostoma caeruleum*), greenside darter (*Etheostoma blennioides*), and fantail darter] appeared and/or increased in abundance.

Marked shifts in the relative abundance of feeding guilds accompanied changes in fish assemblage composition between years 1 and 2, although not at the upstream control reach or OR2 (although note the moderate increase in carnivores at OR1; Fig. 7). The proportion of insectivores in OR3 increased by 19% such that the fish assemblage was almost entirely composed of insectivorous species (Fig. 7f); no omnivorous species were captured in year 2 at this reach. Similarly, OR4 increased in the proportion of insectivores at the expense of omnivorous species (Fig. 7h).

**Fig. 7.** Proportion of fish assemblage by representative feeding guilds at the Olentangy River reaches: (a) OR1 year 1, (b) OR1 year 2, (c) OR2 year 1, (d) OR2 year 2, (e) OR3 year 1, (f) OR3 year 2, (g) OR4 year 1, (h) OR4 year 2.

## Discussion

In the Olentangy and Scioto Rivers of urban Columbus, Ohio, we found that removal of two lowhead dams had significant short-term impacts on both upstream and downstream fish assemblages. Overall, assemblage diversity decreased immediately following dam removal. For upstream reaches, diversity rebounded somewhat in year 2 (note that data are not yet available for downstream reaches in year 2), suggesting that tracking fish assemblage responses over time will be critical in understanding and predicting biotic responses to dam removal. Greater than 80% of the 75,000 dams > 1.8 m high in the United States (Graf 1999) will be beyond their designated life spans by 2020 (Evans et al. 2000). Thus, dam removal has garnered widespread attention as a way to restore river connectivity. Between 1987 and 2007, over 550 dams have been removed in streams and rivers across the United States (Granata et al. 2007) and this trend is expected to continue (reviewed in Poff & Hart 2002). Our results, therefore, represent a timely contribution to a nascent body of literature documenting ecological responses to dam removal and will be valuable in informing and guiding dam removal efforts, particularly in urban settings.

Multiple investigators have reported an increase in fish assemblage diversity and species richness above dam removal sites over short time scales (< 3 years) (Burroughs et al. 2010; Catalano et al. 2007; Gardner et al. 2013; Kanehl et al. 1997; Lenhart 2003). However, in contrast to both these findings and our hypotheses, we observed declines in both *S* and *H*' at the upstream restoration reach (OR3) on the Olentangy River and the upstream reach on the Scioto River (SR1) after dam removal. Active channel restoration conducted in tandem with dam removal in the Olentangy River – including reshaping channel geometry and redeveloping the floodplain – did not appreciably enhance assemblage diversity in the short term. In fact, observed declines in diversity may be attributed in part to disruptive engineering activities associated with the stream restoration. However, restoration disturbance is likely a stronger argument for OR3 than for the Scioto upstream experimental reach (SR1), where activities such as channel dredging and bank reconstruction were confined to the lower section of the study reach only. In addition to the declines of species richness and diversity at these sites, fish abundance was also extremely low (Dorobek and Sullivan, unpublished data), which suggests that the physical disruption may have caused fish to move to less disturbed areas. However, with the end of engineering activities and the potential benefits of channel restoration (increased habitat heterogeneity, increased connectivity with lateral habitats, improved chemical water quality), we do not anticipate these short-term patterns to persist at this reach. In fact, by Y2 (one year after restoration), sensitive darter species not found in these river sections previously (or at very low abundances) had colonized and/or increased in abundance at both OR3 and OR4 (see below for further discussion of fish responses over time).

Fish assemblage responses to dam removal in urban landscapes might be expected to be considerably different than responses in rural landscapes, as shown in other dam removal studies [e.g., Kanehl et al. 1997; Catalano et al. 2007 (agricultural); Gardner et al. 2013 (forested)]. Widely varying rates of upstream erosion and downstream sedimentation in urban rivers (Roberts et al. 2007) demonstrate that factors other than dam removal alone can influence the rate of geomorphic response following dam removal (Gregory et al. 2002; Pizzuto 2002; Doyle et al. 2003b; Schmitz et al. 2009). For example, the Secor Dam (2.5 m in height) on the Ottawa River in northwestern Toledo, Ohio has not retained large quantities of fine-grained sediments and thus the major sedimentological consequence of lowhead dam removal is anticipated to be the mobilization of coarse-grained sand and pebbles (Roberts et al. 2007). In contrast, the removal of two lowhead dams on the Baraboo River (Wisconsin), which is surrounded primarily by agriculture, resulted in the release and subsequent deposition of large quantities of fine sediments 3–5 km downstream (Doyle et al. 2003b). Because geomorphic changes that occur upon dam removal will have direct implications for fish habitat, effects of lowhead dam removal on river fish assemblages are unlikely to be independent of catchment settings (Hart et al. 2002; Tullos et al. 2014). Our findings represent one of the few studies of dam removal in an urban setting, but indicate that fish responses in urbanizing landscapes may be divergent from other landscape contexts in the short-term.

We could not assess the impact of dam removal on downstream fish assemblages for the Olentangy downstream experimental reach (OR4) because of the lack of pre-dam removal data for this study site. However, we did find that removal of the Main Street Dam on the Scioto River led to a significant decrease in species richness and diversity at the downstream Scioto experimental reach (SR2). These findings support our predictions and align with other investigations of lowhead dam removals (Burdick & Hightower 2006; Gardner et al. 2013), which have generally reported downstream reductions in fish species richness, abundance, and biological indices shortly following dam removal. Pulses of sediment may underlie these downstream responses, although the transport of sediment over lowhead dams is not fully restricted given their small size [e.g., release of coarse material to the downstream reach of the Brownsville Dam (~4 m in height) on Oregon's Calapooia River did not quantitatively influence dominant grain size of bed stability; Tullos et al. 2014]. However, other lowhead dam studies have shown that large quantities of sediment can be transported from previous impoundments and be temporarily deposited downstream (Doyle et al. 2003b; Burroughs et al. 2009; Walter & Tullos 2010). Additionally, some fish species (or guilds) are expected to be considerably more sensitive to sediment pulses (e.g., benthic insectivores) than others (Maloney et al. 2008). The 85–97% increase in relative abundance of insectivores in OR4 from years 1 to 2 suggests that an ecologically-impactful sediment pulse immediately downstream of a dam removal may not have been generated in the Olentangy system. Further resolving this issue in our system will require quantitative hydrogeomorphic research to complement existing biological data.

In addition to monitoring fish assemblages immediately after dam removal, we observed changes in fish assemblages over time in the Olentangy River. Following our expectations, richness and diversity increased between years 1 and 2 at OR3 but did not reach pre-dam removal levels and thus it is likely that a stable fish community has not yet been established. Nonetheless, a suite of sensitive darter species [e.g., bluebreast (*Etheostoma camurum*), banded, fantail, greenside, rainbow, and Johnny darters] was present at OR2 by year 1 and OR3 by year 2. For our downstream Olentangy reach (OR4), *H'* (but not *S* or *E*) increased in year 2 (Fig. 6), offering limited support that the effects of dam removal on assemblage diversity (potentially via erosion of impounded sediment transported downstream) may not persist much beyond the immediate term (i.e., one year in this study). However, interpretation of these results is limited given that we lacked pre-dam removal data for this reach.

The mechanisms driving temporal differences in fish responses are not well understood (Kanehl et al. 1997; Doyle et al. 2005; Maloney et al. 2008). A variety of factors can influence the rate and magnitude of ecological change following dam removal, thus making broad predictions of fish assemblage responses over time difficult. The rate of geomorphic response to dam removal will be affected by the quantity and size of sediment stored and the ability of the fluvial system to adjust (Gregory et al. 2002; Doyle et al. 2005), indicating that landscape features may influence post-dam removal changes and the level of ecosystem restoration (Roth et al. 1996; Palmer et al. 2005; Bernhardt & Palmer 2011). The relative mobility of fish species will likely determine how quickly newly-available habitat can be colonized. In addition to habitat changes associated with dam removal, the short life-cycles and relative mobility (via drift) of aquatic macroinvertebrates (an important food source for many stream fishes) suggests that invertebrate assemblages should respond more quickly to dam removal (Stanley et al. 2002) and potentially drive changes in fish assemblage structure. Tullos et al. (2014), for example, found that recovery of benthic macroinvertebrates occurred within the span of a single year following the removal of two dams in Oregon, USA (Brownsville Dam: ~4 m in height, Savage Rapids Dam: ~12.5 m in height). Likewise, we found a greater relative dominance of benthic insectivorous fish across all experimental Olentangy reaches in both year 1 and year 2 (although note that we observed a decline in insectivorous fish one year after dam removal in SR1). Given that other ecological processes (e.g., primary and secondary aquatic productivity, allochthonous inputs of organic matter and subsidies of terrestrial invertebrates) can accompany increased hydrologic connectivity (lateral and longitudinal) as a response to dam removal, further investigation will be required to understand the mechanisms behind shifts in fish assemblages over time.

## Conclusions

Currently, most studies of lowhead dam removal are limited to catchments dominated by agriculture or forests (Bushaw-Newton et al. 2002; Catalano et al. 2007; Maloney et al. 2008; Burroughs et al. 2010) or limited to smaller streams (1st–3rd order) ( Stanley et al. 2007; Gardner et al. 2013). Our study demonstrates that lowhead dam removal can represent a strong pulse disturbance and quantitatively influence fish assemblages in a 5th–6th order urban river system. Overall, we found that dam removal reduced fish assemblage diversity in the short term, both upstream and downstream of dam removals, and that these changes were accompanied by shifts in the relative abundance of individuals and species from different feeding guilds. Post dam-removal restoration activities were associated with depressed assemblage diversity in the short-term, although we anticipate that restoration activities will be beneficial to both taxonomic and functional diversity in the long term (Muotka et al. 2002; Lepori et al. 2005). Though feeding guilds provided insight into the character of fish assemblage responses, additional trait-based metrics might yield meaningful information and help target mechanisms driving current and future shifts in fish assemblages.

Although additional research will be necessary to understand linked biotic-abiotic responses to dam removal and to inform effective and functional dam removal and restoration strategies in a suite of physiographic contexts, our findings provide valuable evidence relative to fish responses across a range of spatial and temporal dimensions associated with dam removal. The multiple dams that still exist within the broader Scioto-Olentangy River system indicate that consideration of the aggregate impact of dams across the catchment will be critical in assessing and predicting ecosystem responses to the removal of single dams. For instance, the presence of additional dams in the system may limit broader recolonization of species into isolated habitats reconnected only to each other via dam removal. Van Looy et al. (2014) posit that for reaches upstream of dams, local habitat quality is deterministic and local measures of restoration may be successful whereas for downstream reaches, multiple stressors demand action at broader spatial scales. Catchment-scale restoration (Bernhardt & Palmer 2011) will likely be necessary for both upstream and downstream reaches in highly managed landscapes such as those of the Scioto River system. Additionally, as responses to dam removal through time may not be expected to be linear (Kanehl et al. 1997; Doyle et al. 2005), our results set the stage for a longer-term investigation to ecosystem responses to dam removal.

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