Short-term consequences of lowhead dam removal for fish-community dynamics in an urban river system

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Abstract

Dam removal has become an increasingly popular river restoration strategy with the aim of reestablishing more natural hydrologic and sediment regimes and increasing habitat availability for aquatic organisms. However, dam-removal research is in its early stages and the ecological impacts are not fully known. For fish, the removal of lowhead dams has been shown to restore hydrologic connectivity and reestablish lotic-type species; yet the magnitudes and rates of recovery are variable across studies. Food webs represent complex trophic networks and are fundamental in understanding the organization of natural assemblages and community dynamics and in describing ecosystem processes. Therefore, incorporating a food-web approach in dam removal studies might be expected to be an important step in quantifying ecosystem responses to dam removal. Here, I investigated the consequences of two lowhead-dam removals in the 5th-order Olentangy and 6th-order Scioto Rivers (Columbus, Ohio) for (1) fish assemblage structure and (2) fish-centered food webs 2-3 years following removal.

The disturbance of dam removal had consequences for both fish assemblages and food-web structure. Upstream fish assemblages experienced a significant decline in species richness in the year following dam removal, which was accompanied by a shift in assemblage composition (ANOSIM: $R = 0.714, p = 0.001$). In the Olentangy River,
assemblage structure shifted significantly over time (between year 1-2) and included the re-colonization of benthic insectivores (ANOSIM: \( R = 0.136, p = 0.019 \)). Species richness increased over time in both the Olentangy (linear mixed model: \( F_{2,16} = 9.70, p = 0.002 \)) and Scioto (linear mixed model: \( F_{2,12} = 26.50, p < 0.0001 \)) Rivers. Species richness returned to pre-dam removal levels in the Scioto River, but was still 58% lower than pre-dam removal levels in the Olentangy River upstream actively restored reach (i.e., where extensive channel modifications occurred) and in other experimental reaches.

Shifts in assemblage composition and species richness were not accompanied by changes in the relative abundance of top predators, intermediate, or basal species; however, these metrics might not capture important shifts in trophic guilds that could have implications for other food-web properties. Similar to species richness, network connectivity decreased significantly at the Olentangy River upstream actively restored reach following dam removal (paired \( t \)-test: connectance \( - t = -6.46, p = 0.023 \); link density \( - t = -13.54, p = 0.005 \)) and did not return to pre-dam removal levels. Whereas link properties decreased on the Scioto River experimental reaches in the year following dam removal, they increased to pre-dam removal levels by second year (linear mixed models: connectance \( - F_{2,12} = 8.38, p = 0.005 \); link density \( - F_{2,12} = 42.26, p < 0.0001 \)). Food-chain length (FCL) – a key measure of food-web architecture – declined from 4.37 to 2.75 in the Olentangy River actively restored reach, and declined significantly in the upstream control and passively restored reaches over time (linear mixed model: \( F_{2,14.7} = 7.43, p = 0.003 \)). FCL also decreased in the upstream reach of the Scioto River by the second year after dam removal (linear mixed model: \( F_{1,6,4} = 28.93, p = 0.001 \); Tukey’s
Significant reductions in channel width (i.e., ecosystem size) and alterations to hydrological connectivity are likely mechanisms driving observed shifts in food-web architecture, wherein larger and more variable habitats support more complex ecological networks. Proximate mechanisms including individual traits of fish species (e.g., body size) may also be important in mediating food-web structure. For example, body length was positively related to FCL (linear regression: $R^2 = 0.221, F = 4.81, p = 0.043$), suggesting that larger individuals support more trophic interactions within a food web and drive network complexity.

The results of this investigation have both applied and theoretical implications for understanding the role of disturbance in structuring fish assemblages and food webs in river systems. More specifically, dam-removal disturbance appeared to strongly influence network stability via a loss of diversity and trophic connections on the Olentangy River. Yet, the rebound of food-web properties in the larger Scioto River by the second year following dam removal suggests that food-web networks in larger river systems could be more resilient than in smaller systems. In the first few years following dam removal, active channel restoration did not enhance fish community diversity or FCL and exhibited a less complex fish-based food web than in a passively restored reach, although the benefits of this restoration may take additional time to be realized. The number of small dam removal projects is expected to grow considerably in the coming years, and increasing our understanding of the consequences of dam removal for the ecological integrity of river ecosystems is critical for effective river conservation and management.
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Chapter 1: Background and Literature Review

Dam removal is an increasingly popular restoration and management technique for river ecosystems. However, significant hydrogeomorphic changes associated with removal can act as a disturbance (Pickett & White, 1985), with numerous consequences for fish community dynamics. In particular, the consequences of the pulse disturbance (sensu Lake, 2000) of lowhead dam removal (Tullos et al., 2014) for fish communities are not fully resolved (Bednarek, 2001). Dam removal has been shown to lead to shifts in fish-assemblage structure (Stanley & Doyle, 2003; Cumming, 2004; Kornis et al., 2015); however, these investigations have yielded variable results and are likely dependent on the size of the dam, river, and reservoir as well as the amount of sediment stored behind the dam and its grain size (O'Connor et al., 2015). Even further, the consequences of changes in fish-assemblage structure for community interactions and ecological processes have not been fully investigated.

Shifts in fish assemblages could have further consequences for food-web structure. Food webs are complex ecological trophic networks that are fundamental to understanding the organization of natural assemblages and population dynamics and have been widely related to ecosystem processes such as nutrient cycling, and contaminant and energy transfers (Pimm, 1982; Sabo et al., 2009; Sullivan & Rodewald, 2012). Furthermore, food webs are structured by both biotic and abiotic interactions and can
identify potential mechanisms associated with disturbance that lead to shifts in biotic assemblage structure. Several properties can be used to evaluate food-web structure (e.g., proportion of top predators, predator:prey ratios, food-chain length, connectance; Williams & Martinez, 2000; Bersier et al., 2002; Dunne, 2004); yet, to my knowledge these properties have not been evaluated within a pulse-disturbance context in stream ecosystems.

My research contributes to current understanding of the ecological consequences of lowhead dam removal. From a theoretical perspective, I explore how dam removal acts as a disturbance over time (2-3 years following dam removal) on fish community diversity and function. I also explore the consequences of dam removal for fish-centered food webs including effects on food-chain length and network complexity (e.g., connectance, link density). From an applied perspective, I anticipate that this research will further inform dam removal strategies, particularly in urban landscapes, where there has been comparatively little research. Additionally, I compare active (i.e., engineering) versus passive (i.e., left to naturally adjust) channel restoration approaches, which is uncommon in dam-removal studies.

1.0 Dams and dam removal

1.1 The effects of dams on river systems

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). According to Graf (1999), there are nearly 75,000 dams in the United States alone, a majority of which are
small dams. Altered hydrologic regimes associated with dam operations are one of the leading threats to freshwater fauna (Richter et al., 1997). Also important is the sediment regime, which is associated with channel morphological bed conditions and heterogeneity, disturbance regime, community structure, and chemical water quality (Jacobson et al., 2009; Wohl et al., 2015). Dams impact the natural flow and sediment regimes, which further affect the ecological integrity (i.e., the structure, composition, and function of an ecosystem as compared to reference ecosystems operating within bounds of natural or historic disturbance regimes; sensu Karr, 1999) of river systems (Poff et al., 1997). More specifically, the lack of longitudinal connectivity of sediment and water restricts habitat availability for aquatic organisms (Bellmore & Baxter, 2014; Wohl et al., 2015). Therefore, the physical and chemical alterations caused by dams could have important implications for aquatic biota.

For fish, the impacts 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., 1996a). Dams not only disrupt the natural hydrologic regime, but also serve as barriers to fish migration and dispersal (Hayes et al., 2008). Many migrating species cannot access important spawning grounds (Morita & Yamamoto, 2002; Aadland et al., 2005; Lake et al., 2012), leading to depressed reproductive success and population sizes. This is especially true for anadromous species including Pacific salmonids (Brenkman et al., 2012), the Australian grayling (Prototroctes maraena, Gehrke et al., 2002), and
several sturgeon species (Parsley & Beckman, 1994; Ferguson & Duckworth, 1997; Kynard, 1997; Jager et al., 2001). Much attention has been drawn to the effects of large dams on important anadromous commercial fish species, especially those that face threats of endangerment or extinction (Pess et al., 2008; Burroughs et al., 2010).

Non-migratory, resident fish species have received less attention, but they, too, can be severely impacted by dams. Habitat fragmentation reduces dispersal of resident fish species into suitable habitats, which further disrupts longitudinal flows of energy and nutrients (e.g., nitrogen, phosphorous; Santucci et al., 2005; Fjeldstad et al., 2012). 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 (Dudley & Platania, 2007; Roberts et al., 2013) and reductions in genetic diversity (Morita & Yokota, 2002; Tsuboi et al., 2010).

1.2 Lowhead vs. large dams

Although dams vary considerably in size relative to both height and width, criteria used to classify dams by size are 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 this study, lowhead dams are defined as run-of-river dams with a hydraulic head ≤ 7.5 m (Stanley & Doyle, 2002), with reference to “large” dams as
storage dams > ~7.5 m in height. Within this framework, significant attention has been directed towards large dams (Hill et al., 1994; Shuman, 1995; Pess et al., 2008), with an increase in the number of studies on the effects of lowhead dam removal on fish-community dynamics in recent years; however, additional research is needed (O'Connor et al., 2015). 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). Of the 1,483 dams in the state of Ohio, nearly 41% percent are < 7.62 m. Yet, this estimate does not include low-hazard and other small water-control structures potentially underestimating the impact of run-of-river dams in the state.

The ecological impacts of dams vary and might be expected to be primarily determined by the volume of water and sediment stored by the dam (O'Connor et al., 2015). The amount of water impounded by a dam differs greatly from one site to another. Small run-of-river dams direct and control streamflow and, therefore, comparatively little water is stored behind the dam (Baxter, 1977). However, lowhead dams can store sufficient quantities of sediments that consequently alter stream geomorphology (Doyle et al., 2003b; Helms et al., 2011). Dams disrupt connectivity altering the natural hydrologic regime and transport of sediments, which affects habitat availability. Additionally, in-stream habitat quality and availability differs upstream and downstream of the dam especially because dams generally establish lentic environments in their reservoirs. Changes in hydrogeomorphology depend on dam size and function (Pizzuto,
Whereas large dams have substantial effects on upstream and downstream areas (Graf, 2005), lowhead dams can also alter upstream and downstream habitat availability (Brown et al., 2004; Santucci et al., 2005).

Lowhead dams can 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). Gardner et al. (2013) found that species richness was always greatest immediately below the Mill Dam (3-m high) on the Sedgekedunk Stream (Penobscot River, Maine), most likely because it was the only site readily accessible to migrating fish, which was further supported by the presence of migratory and resident fish species. In addition to the physical barriers imposed by dams, declines in richness and abundance upstream of 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). In other words, lowered species richness and abundance observed in upstream impoundments could be due to either the disruption of fish movement or fragmentation of the hydrologic and sediment regimes that leads to impaired habitat and chemical water quality (Santucci et al., 2005; Hayes et al., 2008). The relative impact of lowhead dams on fish-assemblage structure is likely mediated by landscape features (e.g., land use and land cover, riparian buffers), variability in natural processes (e.g., flow regime, sediment transport
biogeochemical cycling), and management practices (e.g., controlled water releases) (Poff & Hart, 2002; Cumming, 2004), underscoring the importance of the broader environmental context.

1.3 Ecological impacts of dam removal

Given the effects of dams on the hydrologic regime, their removal could lead to significant hydrogeomorphic changes that could act as an ecologically meaningful disturbance (sensu Resh et al., 1988) with potential consequences for fish-assemblage structure (Bednarek, 2001; Gregory et al., 2002; Doyle et al., 2005). Disturbances include any discrete event that has consequences for ecosystem, community, or population structure as mediated by changes in resources, substrate availability, or the physical environment (Pickett & White, 1985). Conceptualizing dam removal as a disturbance frames changes in ecological processes within a theoretical context. Dam removal has been proposed as a pulse disturbance (i.e., short-term and sharply delineated disturbances; Lake, 2000) by Tullos et al. (2014) and subsequently by Dorobek et al. (2015), which may have strong consequences for aquatic taxa including fish (Stanley & Doyle, 2003; Stanley et al., 2007; McLaughlin et al., 2013). However, the potential impacts of dam removal – and particularly of lowhead dam removal – remain poorly resolved. The removal of large dams has been shown to benefit migratory fish species by restoring fish passage (Lake et al., 2012; Pess et al., 2014; Raabe & Hightower, 2014). However, the effects of lowhead dams, and by extension their removal, are unlikely to be comparable with larger dams (Hart et al., 2002; Poff & Hart, 2002). Yet, there is little
consensus as to the consequences of lowhead dam removal for resident fish assemblages (Gangloff, 2013; Kornis et al., 2015), although ecological impacts of small dam removal projects have been observed (Doyle et al., 2003b; Stanley & Doyle, 2003).

Resident fish assemblages will likely be affected by habitat availability (Bednarek, 2001; Maloney et al., 2008; Burroughs et al., 2010), which will be determined by the significant hydrogeomorphic changes that can occur immediately after dam removal (Im et al., 2011). Most dams, because they block streamflow, become areas of sediment storage. Upon removal, sediments that accumulate behind the dam are either flushed downstream or exposed on channel banks in the previous impoundment (Pizzuto, 2002; Doyle et al., 2003a; Stanley & Doyle, 2003) resulting in varying hydrogeomorphic changes in upstream and downstream reaches (Gartner et al., 2015). Differences in upstream and downstream shifts in hydrogeomorphology could have variable effects on fish assemblages. With small run-of-river dams, sediments released after the removal of lowhead dams can be transported and deposited downstream relatively quickly (i.e. less than one year; Stanley et al., 2002), which could alter habitat availability. Further, these sediments can contain heavy metals, polychlorinated biphenyls (PCBs), and other contaminants that can adversely affect fishes, other aquatic biota (e.g., macroinvertebrates), and humans (Gray & Ward, 1982; Shuman, 1995). Despite the general model of downstream transport of sediments following dam removal, patterns and rates of sediment transport are highly variable (Doyle et al., 2005) and will depend on factors like catchment and local land-use, sediment storage quantities, sediment characteristics (Doyle et al., 2003), dam size and function, and dam removal techniques.
(Bednarek, 2001; Pizzuto, 2002) making it difficult to predict how dam removal will affect habitat availability for fishes.

Some studies suggest that fish will respond relatively quickly to dam removal whereby reservoir species will be washed downstream and riverine species will become reestablished in the previous impoundment (Kanehl et al., 1997; Bushaw-Newton et al., 2002; Stanley & Doyle 2003). To date, evidence suggests that fish species richness, diversity (Catalano et al., 2007; Burroughs et al., 2010), and biomass (Gardner et al., 2013) tend to increase upstream of previous dam locations, returning to lotic-type communities (Bushaw-Newton et al., 2002; Maloney et al., 2008). The downstream transport and aggradation of sediments could have negative consequences for fish assemblages through habitat homogenization, loss of chemical water quality, or reductions in benthic macroinvertebrates as food sources (Im et al., 2011). In fact, downstream invertebrate assemblages have been shown to decline in species richness, abundance, and diversity shortly following dam removal (Catalano et al., 2007; Gardner et al., 2013; Magilligan et al., 2016). However, fish assemblages may continue to respond to hydrogeomorphic changes over longer periods of time (e.g., five years; Kanehl et al., 1997). Although some investigators have observed reductions in fish diversity for several years post dam removal in downstream areas (Maloney et al., 2008; Burroughs et al., 2010), others have found increases < 2 years after initial declines (Dorobek et al., 2015).

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 within a year after dam removal (Burdick & Hightower, 2006; Catalano et al., 2007; Fjeldstad et al., 2012; Gardner et al., 2013; Magilligan et al., 2016), others have demonstrated that quantitative changes occurred only after several years (Doyle et al., 2005; Maloney et al., 2008; Stanley et al., 2007). 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., decrease in abundance of common carp), whereas for others (e.g., smallmouth bass increase) there appeared to be a longer time lag following dam removal (Kanehl et al., 1997). This suggests that both short- and long-term monitoring are necessary to understand how fish assemblages respond to dam removal.

Helms et al. (2011) also detected variability in recovery time, but among different taxa. Mussel assemblages differed significantly among reach locations in streams with relict dams whereas fish and crayfish assemblages did not differ, indicating recovery of these taxa, but not of mussels. In fact, Doyle et al. (2005) posits two models for ecosystem recovery representing both full and partial ecosystem recovery that demonstrate the variation in recovery rates of major ecosystem components (Figure 1.1). This model has important implications for both dam-removal effects on not only individual taxa, but also on the ecological interactions and monitoring timescale of
ecosystem responses following dam removal. Knowing the trajectory of ecosystem response will be critical in evaluating the success of dam-removal projects (Doyle et al., 2005).

**Figure 1.1.** Conceptual framework of ecosystem recovery following dam removal relative to pre-dam removal conditions. Diagram includes two frameworks: (A) full recovery of ecological and geomorphic variables return to pre-dam removal conditions versus (B) partial recovery where only some ecological and geomorphic variables return. From Doyle et al. (2005).

2. **Food webs**

   Food webs are networks of consumer-resource interactions among a group of organisms, populations, or aggregate trophic units (Dunne et al., 2002a). Direct trophic
relationships between consumers and their resources as well as indirect, non-trophic relationships are important drivers of food-web structure; however, these processes can be influenced by other factors. Food webs are fundamental to understanding the organization of natural assemblages and population dynamics (Polis & Winemiller, 1996). Even further, food webs play a key role in understanding and describing ecosystem processes such as primary production, nutrient cycling, and decomposition (de Ruiter et al., 2005).

2.1 Food-web properties

Food webs can be described in multiple ways that include both theoretical and empirical approaches (Pimm, 1982; Polis & Strong, 1996; Bersier et al., 2002; Schmidt et al., 2007). At the broadest level, food webs can be described as connectance webs, energy-flow webs, or interaction webs (Pimm, 1982; Polis & Strong, 1996). Connectance, or topological, webs include a static description of feeding links among species or guilds and are produced from predatory-prey binary matrices that indicate potential pairs of predator prey interactions. Energy-flow food webs also show trophic links among species; however, these webs include the magnitude of energy or biomass transferred between interactions throughout the food web providing a more quantitative approach to understanding food-web function. Yet, energy-flow food webs cannot predict community dynamics. Interaction webs may be more useful in describing key trophic interactions by taking into account functional traits and trophic interaction effects on community structure and ecosystem functions (Sabo et al., 2009).

Quantitative properties of food webs can also be used to describe ecologically
relevant information from food-web structure and composition. These properties include species (section 2.1.1), web-interdependence (section 2.1.2), link (section 2.1.3), and chain properties (Bersier et al., 2002). Link properties (e.g., connectance, link density) are determined from predator-prey matrices and have implications for network structure and stability (Deangelis, 1975; Dunne et al., 2005; Warren, 1990). Chain properties, like food-chain length, describe trophic linkages and energy transfers between consumers and resources. These properties can be used both empirically and theoretically to understand factors that affect community structure, population dynamics, and ecosystem function (Table 1.1).
Table 1.1. Description of food-web properties used in the current research, modified from Bersier et al. (2002) and Romanuk et al. (2006).

<table>
<thead>
<tr>
<th>Food-web properties</th>
<th>Description</th>
<th>Metrics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Richness of taxa and species in a food web; also includes proportions of top predators, intermediate, basal, and herbivorous species</td>
<td>species and taxa richness, % top predators, % basal species</td>
</tr>
<tr>
<td>Web interdependence</td>
<td>Considers species distributions and dispersal patterns as potential drivers of community structure and species interactions</td>
<td>homogenization, beta diversity (see Koleff et al. 2003)</td>
</tr>
<tr>
<td>Link</td>
<td>Quantifies trophic-interaction patterns to describe network complexity based on number of trophic links in relation to taxonomic richness</td>
<td>connectance, link density, degree distributions</td>
</tr>
<tr>
<td>Chain</td>
<td>Describes the number of trophic links between consumers and the base of the food web determined by the relative trophic position (TP)</td>
<td>mean trophic position, food-chain length, standard deviation of trophic position</td>
</tr>
</tbody>
</table>
2.1.1 Species properties

Species properties consider the number (i.e., richness) and character (e.g., top predators, herbivores) of taxa as a way to describe the functional role of food-web constituents and indicate the complexity of trophic interactions (Bersier et al., 2002). Species can be described as either top predators (i.e., having prey, but no predators), intermediate (i.e., having both predators and prey), or basal (i.e., having only predators) based on their feeding relationships within the food web (e.g., Kautza & Sullivan, In press). Quantifying the relative abundance of these trophic roles can help describe the type of trophic interactions that are important in shaping other food-web properties (Cohen, 1978). Further, changes in species properties could serve as potential mechanisms driving shifts in other food-web characteristics (Paine, 1966) as described by Post and Takimoto (2007; See Sections 2.1.3, 2.2.1, and 3.1).

2.1.2 Web-interdependence properties

Web-interdependence properties include beta diversity and biotic homogenization, which are processes that have important implications for community and food-web structure (Dar & Reshi, 2013). Biotic homogenization is a globally-common phenomenon that includes the loss of taxonomic regional distinctiveness through the replacement of local taxa with non-indigenous or widespread species (McKinney & Lockwood, 1999). Homogenization has been shown to lead to an increase in species richness at the local level (i.e., alpha diversity), but a loss of diversity at the global level induced by human factors (Dar & Reshi, 2013). Fish fauna across the United
States have shown increasing homogenization due to introduction of non-native sport fish and the accidental transport of alien species (Rahel, 2000), but other environmental factors could be at play (Devictor et al., 2008). Whereas much attention has been focused on the increasing distributions of non-native species, the introduction of native invaders that replace more sensitive endemic species is a growing concern (Helfman, 2001). Replacement of endemics by highly tolerant, widely-distributed species can lead to reduced functional diversity with implications that cascade throughout the food web (Clavel et al., 2011).

Homogenization has been shown to have implications for beta diversity (i.e., species turnover across spatial and/or environmental gradients; Whittaker, 1972) with observed declines in beta diversity as a result of increased local or alpha diversity. There are numerous metrics that measure beta diversity based on species presence-absence data (Koleff et al., 2003). Indices of similarity (e.g., Sørensen, Jaccard) have been used to evaluate beta diversity as expressions of continuity between sites and over time, but can also provide some insights to homogenization (Dar & Reshi, 2013). In general, as beta diversity increases, the community composition of different areas increasingly diverges (i.e., greater difference in species composition). Combined with alpha diversity, beta diversity can help describe species heterogeneity of a defined area (Wilson & Shmida, 1984). More specifically, beta diversity can be used to compare diversity and interdependence between sites. Therefore, incorporating beta diversity should help describe the role of longitudinal connectivity in shaping food-web structure.
2.1.3 Link properties

Link properties consider the number of trophic interactions relative to species richness of a food web including link density (i.e., number of links over species richness) and connectance (i.e., number of links over the maximum possible links; Martinez, 1991). These properties have been widely studied to help understand the relationship between network complexity and community stability (Dunne et al., 2002a). Additionally, connectance may be tied to other food-web properties (e.g., degree distributions, interaction strengths) that are thought to be related to network stability (Poisot & Gravel, 2014). Initial hypotheses claimed that increasing network complexity (i.e., increasing the number of links) would lead to more stable communities (MacArthur, 1955). MacArthur further claimed that the number of links increases with assemblage diversity, thus connecting community stability with species richness and number of trophic interactions (Dunne et al., 2005). Soon after, May (1972) challenged this hypothesis and found that community stability can increase with an increase in species richness as long as connectance decreases.

Several decades of research followed to try to solve the complexity-stability debate (Paine, 1988; Lawton & Warren, 1989) with several factors emerging that could influence the relationship between connectance and diversity including interaction strength, aggregation of taxa, intraspecific interactions (i.e., cannibalism), sampling effort, and resolution of the food web (Yodzis, 1988; Martinez, 1991; Polis, 1998; Bersier et al., 1999). In general, network complexity might be expected to play an integral piece in the diversity-stability relationship (McCann, 2000; Estrada, 2007; Gravel et al., 2011).
because it serves as the mechanism that links diversity to community stability, but the relationship between link properties, species richness, and stability remains unresolved (Figure 1.2). Although universal patterns are not conclusive, understanding the relationship between network structure of food webs and their ability to handle perturbations is central to ecology (May, 2001; See Section 3). Even further, environmental factors affecting food-web structure are of particular concern (Briand, 1983; Dunne et al., 2005).

![Figure 1.2. Relationship between number of links and species. From Dunne et al. (2005).](image)

2.1.4 Chain properties

A food chain describes a distinct path from a basal taxon to higher trophic levels (Pimm & Kitching, 1987). Several properties can be used to evaluate food chains including mean, maximum, and standard deviation of chain length (Bersier et al., 2002).
2.1.4.1 Food-Chain Length

Food-chain length (FCL) – a measure of energetic pathways and ecological structure (Sabo et al., 2009) – is a widely used measure that considers the number of links between trophic consumers and the base of the food web. Food-chain length is determined from the maximum trophic level in a food web, which commonly has been determined by qualitatively assigning an approximate position based on a species’ feeding relationships or from connectance food webs (Post, 2002a). However, using this approach can underestimate the energetic importance of certain trophic interactions within a food web and fail to capture actual feeding relationships (Vander Zanden et al., 1997), which are highly dependent on other trophic interactions and environmental factors. Even further, the presence of cannibalism and loops (e.g., A eats B and B eats A) can complicate FCL using these methods (Williams & Martinez, 2000). Therefore, more quantitative approaches (e.g., stable-isotope analysis) have been increasingly used to determine reliable measures of FCL (Vander Zanden et al., 1997; Schmidt et al., 2007).

Food-chain length also provides further insights on the relationship between environmental factors (e.g., disturbance regime, ecosystem size, productivity) and ecosystem processes (Power et al., 1996b; Post et al., 2000; Takimoto et al., 2008; McHugh et al., 2010; Sullivan et al., 2015). Several hypotheses have been proposed to determine the environmental determinants of FCL:

*Dynamical-constraints hypothesis:* According to the dynamical-constraints
(Jenkins et al., 1992), or stability, hypothesis (i.e., disturbance hypothesis), food chains will be shorter in highly variable environments. Pimm and Lawton (1977) found that longer food chains were less stable (i.e., longer return times for equilibrium states) and that shorter food chains should be found in systems that experience frequent and extreme disturbances. Sterner et al. (1997) expanded on the Pimm and Lawton (1977) models by varying number of species, trophic levels, feeding configurations, and location and number of self-damping (i.e., intraspecific interaction where a species experiences negative feedback from its own density independent from the density of all other species in the food web; Sterner et al., 1997) terms and found that self-damping terms had the greatest effect on food-web stability.

In addition to the paucity of theoretical support for the dynamical-constraints hypothesis, there is a lack of empirical evidence that disturbance is a stand-alone factor limiting FCL (Walters & Post, 2008; Takimoto & Post, 2013) especially in river systems (Townsend et al., 1998; Walters & Post, 2008; Warfe et al., 2013). Rather, it is likely that disturbance, characterized by gradients of predictability, frequency, and magnitude among others (Poff, 1992; McHugh et al., 2010), interacts with additional factors to affect mechanisms (e.g., removal of intermediate predators) that affect FCL (Post & Takimoto, 2007; Power et al., 2008). Furthermore, connectivity in river systems could override local determinants (e.g., productivity, ecosystem size) of FCL (Warfe et al., 2013).

Still, streams are highly dynamic systems. Streams have consistently been shown
to support shorter food chains than lakes and marine ecosystems, which suggest that disturbance might limit aquatic FCL (Vander Zanden & Fetzer, 2007). At a local scale, however, within-stream variation in FCL is probably limited by other factors.

**Productivity hypothesis:** The productivity hypothesis (Pimm, 1982), or the energetic-constraints hypothesis (Oksanen *et al.*, 1981), posits that FCL is limited by the basal energy supply (usually primary producers in aquatic systems) due to energy losses that occur with each trophic transfer. In other words, longer food chains should be found in more productive systems. Contradictory results have been presented as to whether energy availability regulates FCL (Jenkins *et al.*, 1992). It is possible that studies that have not found a relationship between productivity and FCL (e.g., Briand & Cohen, 1987; Vander Zanden & Fetzer, 2007; Warfe *et al.*, 2013) did not include systems with sufficiently low levels of available energy necessary to limit higher trophic levels (Post, 2002a). Therefore, basal energy might only be important in more extreme circumstances (Kitching & Pimm, 1985; Jenkins *et al.*, 1992; Post, 2002a). However, primary productivity has been shown to be related to food-web structure in streams. Thompson and Townsend (2005) found that more productive streams (e.g., grassland streams) had more algal species, displayed greater internal connectance (see Table 1.1), and had longer food chains. Less productive streams (e.g., forested streams) showed the opposite trends and included lower predator-prey ratios. Yet, these
results could be driven by other factors that could affect FCL. For example, Briand and Cohen (1987) found that three-dimensional ecosystems (e.g., forest canopy, pelagic zones) supported longer food chains than two-dimensional ecosystems (e.g., grasslands or lake bottoms). These investigators postulate that the effect of dimensionality might be related to the likelihood of predator-prey interactions. Therefore, the different stream types tested by Thompson and Townsend (2005) might exhibit dimensionality described by Briand and Cohen (1987) rather than an effect of productivity alone.

_Ecosystem size/productive-space hypotheses:_ Evidence has also been presented supporting ecosystem size as a driver of FCL (McHugh et al., 2010; Sabo et al., 2010). The ecosystem size hypothesis predicts that larger systems should have longer food chains due to greater habitat heterogeneity and the capacity to support compartmentalized food webs (Post et al., 2000). Ecosystem size might also affect FCL by providing more basal energy resources. The productive-space hypothesis (Schoener, 1989) suggests that FCL should increase as a function of total ecosystem productivity (i.e., the product of ecosystem size defined by area or volume and a measure of per unit size productivity or resource availability). This hypothesis can be difficult to test because variation in FCL could be the result of resource availability, ecosystem size, or both (Vander Zanden & Fetzer, 2007). Several studies have found a strong effect of ecosystem size, but little evidence for an effect of resource availability on FCL (Spencer & Warren, 1996; Vander
Ecosystem size likely influences FCL through its relationship with species richness and the history of community organization (Cohen & Newman, 1991; Post et al., 2000). McHugh et al. (2010) found that ecosystem size was positively correlated to FCL as well as species richness. Further, changes in species richness and the identity of the top predator suggested that stream size influenced FCL primarily through and effect on fish community structure. While FCL has not been found to be correlated with species richness (Sabo et al., 2009), the addition of taxa is likely a major mechanism for food-chain lengthening (Vander Zanden et al., 1999; Post & Takimoto, 2007). Yet, the effect of ecosystem size on FCL in streams has been shown to have variable results (Thompson & Townsend, 2005; Vander Zanden & Fetzer, 2007; Hoeinghaus et al., 2008), suggesting that other factors could be at play.

**Ecosystem structure:** Sullivan et al. (2015) found a weak, but positive relationship between FCL and drainage area, a measure of ecosystem size; however, they found a stronger relationship between FCL and measures of ecosystem structure (e.g., number of tributary junctions, distance from the downstream confluence). However, drainage area was correlated with measures of ecosystem structure including stream order, stream length, confluence distance, and number of tributary junctions. These authors hypothesize that catchment structural characteristics integrate both ecosystem size as well as more mechanistic drivers.
of FCL. In particular, food-chain lengthening likely occurred through either insertion of intermediate taxa or changes in omnivory described by Post and Takimoto (2007) that was supported by either alterations in habitat volume, greater connectivity, or shifts in the disturbance regime. In stream systems that are heavily impacted by dams, ecosystem structure may be a weaker driver of FCL especially because dams disrupt the natural hydrologic regime (including hydrologic disturbance), alter habitat volume, and limit connectivity. Yet, no studies to date have examined the effect of dam removal on FCL.

2.2 Stable-isotope analysis

Stable-isotope analysis (SIA) is increasingly used in ecology to analyze food-web structure and explore trophic interactions in ecosystems (Vander Zanden et al., 1999; Post et al., 2000). The naturally-abundant stable isotopes of carbon ($^{13}$C) and nitrogen ($^{15}$N) have been used in aquatic studies especially in regards to estimating trophic position (TP) of fish (Vander Zanden & Rasmussen, 1999; Finlay, 2001; Post, 2007). Stable-isotope analysis provides a robust technique for estimating TP and integrates important energetic transfers over time and space (Polis & Strong, 1996; Finlay et al., 2002; Post, 2002a; Sabo et al., 2009).

Trophic position is estimated from the process of nitrogen enrichment (Vander Zanden et al., 1999), which is estimated to be 3-4 ‰ of the isotopically-heavy $^{15}$N (Cabana & Rasmussen, 1996):

$$TP = \lambda + \frac{(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{base}})}{\Delta_n}$$
where \( \lambda \) is the trophic position of the selected isotopic baseline; \( ^{15}\text{N}_{\text{consumer}} \) and \( ^{15}\text{N}_{\text{base}} \) are the \( ^{15}\text{N} \) signatures for the consumer and baseline, respectively; and \( \Delta_n \) is the fractionation rate of nitrogen. While some variation exists around this value (Kling et al., 1992; Vander Zanden & Rasmussen, 1999; Ponsard & Arditi, 2000), 3.4‰ is commonly used in aquatic food-web studies; while 0.4‰ is commonly used for C enrichment (Post, 2002a). Because aquatic consumers can be reliant on both terrestrial and aquatic food sources, a two-source mixing model to determine TP is often used for aquatic food webs (Post, 2002a):

\[
TP = \lambda + (^{15}\text{N}_{\text{consumer}} - [^{15}\text{N}_{\text{base}1} \times \alpha + ^{15}\text{N}_{\text{base}2} \times (1 - \alpha)]/\Delta_n
\]

where \( \alpha \) is the proportion of N acquired from baseline 1 (base1). To determine \( \alpha \), the assumption is that C and N move through the food web similarly in order to use a 2-end-member linear mixing model:

\[
\alpha = (^{13}\text{C}_{\text{consumer}} - ^{13}\text{C}_{\text{base}2})/(^{13}\text{C}_{\text{base}1} - ^{13}\text{C}_{\text{base}2})
\]
Figure 1.3. Frequency of enrichment values of (A) $\delta^{15}N$ (A) and (B) $\delta^{13}C$ as estimated by Post (2002a).

2.3 “Fish-centered” food webs

Fish form a central component of aquatic food webs (Romanuk & Levings, 2005), which are critical in understanding ecological integrity because of their strong associations with ecosystem function (Sabo et al., 2009) and community stability (Deangelis, 1975; Pimm & Lawton, 1977). Romanuk et al. (2006) looked at regional and local influences of the relationship between species composition of riverine fish
assemblages and food-web structure. Food-web properties were evaluated from fish-assemblage data for each region using a theoretical approach to describe changes in food-web structure based on differences in fish assemblage composition. This approach could provide a reliable method to evaluate food-web structure without the resolution necessary to evaluate all taxonomic levels of the food web.

3. Disturbance and Aquatic Food Webs

Disturbance is an important process that regulates structure across levels of an ecosystem; which is especially true for stream and river ecosystems, which are in constant state of biotic and abiotic flux due to hydrologic and sediment regimes (Resh et al., 1988). Disturbance can be measured based on its intensity, frequency, and magnitude, and duration. In stream systems, predictability is an important factor where unpredictable changes in hydrology or substrate movement act as ecologically-meaningful disturbances (Townsend et al., 1997). Therefore, characteristics of hydrologic discharge (e.g., timing, magnitude) and the percent of bed movement are typically used to measure disturbance (Richter et al., 1996). Ecosystem stability refers to the probability of species persisting in response to disturbance (Walker, 1995); however, the function of the species may play a larger role than the number of species in determining community response to disturbance. Robustness is a property that allows a system to maintain its function despite perturbation (Dunne et al., 2002b; Kitano, 2004). Ecological resilience is the magnitude of disturbance that a system can experience before it shifts into a different state (Holling, 1973). Even further, resilience refers to the degree at which some ecological variable returns to pre-
disturbance levels (Nimmo et al., 2015).

Whereas disturbance has been shown to affect biodiversity, its effect on ecosystem processes is not as well understood (Hooper et al. 2005). The effects of these disturbances will likely depend on the complexity of the ecosystem impacted as well as the number and function of species lost (Sole & Montoya, 2001; Dunne et al., 2002b; Montoya & Sole, 2003). This is of particular concern because declines in diversity could simplify ecological communities and, thus, the functions they can perform (McCann, 2000; Tylianakis et al., 2010; Thompson et al., 2012a). Therefore, understanding how a disturbance, like dam removal, impacts food-web structure could provide insights to the relationship between biodiversity, community stability, and ecosystem function. Several approaches have been taken to try and understand how disturbance may affect aquatic food webs:

_Trophic cascades:_ Disturbances could influence individual species or particular functional groups that could have further consequences for other food-web members. Even further, disturbance can regulate food webs through bottom-up or top-down controls (Power, 1992; Power et al., 1996b). Wooton (1996) found that changes in flooding disturbances increased predator-resistant grazing insects densities, which had further negative implications for both lower (i.e., algae) and higher (i.e., predators) trophic levels. Evaluating the effects of the removal/addition and/or changes in abundance of individual species could suggest further mechanisms that regulate other food-web properties.
Food-chain length: Disturbance has been proposed as a regulator of FCL, although varying support has been found in stream ecosystems (Townsend et al., 1998; Walters & Post, 2008; McHugh et al., 2010). However, these investigations included several types of disturbance, which likely affect FCL in different ways (Sabo et al., 2009). Additionally, many of these studies used a connectance-based mean FCL versus stable-isotope analysis to determine maximum trophic position. Whereas disturbance may not directly regulate FCL, it might be expected to influence other factors that in turn affect FCL (Post, 2002a). For example, disturbance could affect habitat availability and quality for prey items (Marks et al., 2000; Parker & Huryn, 2006). Post and Takimoto (2007) proposed two proximate mechanisms by which FCL could be regulated:

i. Addition/removal of a top predator

ii. Change in the trophic position of the top predator

These authors further proposed that the TP of the top predator (ii, above) could be influenced by the following:

i. Addition/removal of intermediate predators (or basal species) (i.e., insertion mechanism)

ii. Change in the degree of trophic omnivory by the top predator (i.e., omnivory mechanism)

iii. Change in the trophic position of intermediate predators that are prey for top predators
Thus, environmental determinants of FCL (e.g., disturbance) likely affect FCL differently depending on how they influence the mechanisms proposed by Post and Takimoto (2007; Sullivan et al., 2015).

*Ecological network structure:* The consequences of a disturbance for network structure are largely influenced by stability of species persistence. Therefore, understanding the relationship between food-web structure and biodiversity could help predict the effects of disturbance on network complexity. One study that modeled the effects of species extinctions on food-web stability found that robustness (i.e., stability) increased with food-web connectance, but was independent of species richness and degree of omnivory (Dunne et al., 2002b). Although there is still debate as to the relationship between connectance and stability (see Section 2.1.3), it is likely linked to other characteristics of network-structure that determine the persistence of species within communities (e.g., compartmentalization; see following description). Compartmentalization refers to a set of highly interacting nodes (Poisot & Gravel, 2014). The level of compartmentalization could determine how food webs respond to disturbance (Dunne, 2004; Dunne et al., 2005). Highly compartmentalized food networks are thought to be more stable (Krause et al., 2003). A loss of highly connected nodes can lead to instability where local species extinctions are associated with less compartmentalization (Sole & Montoya, 2001). Further, perturbations (e.g., species loss) are likely contained within highly connected compartments, which
limit cascading effects throughout the network (Stouffer & Bascompte, 2011). The strength of interactions could also be important in predicting the effect of disturbance on aquatic food webs. Network complexity could further influence the effect of disturbance on other food-web properties. For example, a study on the effect of drought conditions on FCL concluded that contrasting effects of reduced streamflow velocity on size structure and FCL were mediated by food-web complexity (Walters & Post, 2008).

4. Study System

The study system of the research presented in this thesis is located in central Ohio, USA and consists of the middle section of the Scioto River and the lower section of its principal tributary, the Olentangy River. The Olentangy River is a 5th-order, 156-km tributary of the Scioto River, where it joins the Scioto River just south of The Ohio State University campus. The Scioto River is a 6th-order, 372-km tributary of the Ohio River. The stretch of the Scioto River used in this study begins just downstream of the Olentangy-Scioto confluence to Berliner Park (Columbus, Ohio). The section of the Olentangy River used in this study extended from shortly upstream of the confluence with the Scioto River to the Wilma H. Shiermeier Olentangy River Wetland Research Park (ORWRP).

The landscape surrounding these sections of the Olentangy and Scioto Rivers is highly urbanized with extensive human modifications. The system is channelized and includes several dams including the lowhead Dodridge Street dam near the ORWRP and
the Greenlawn Avenue dam downstream of downtown Columbus (Figure 1.1). Two dams were removed during the course of this study including the 5th Avenue (2.5 m in height, Olentangy River) and Main Street (4.1 m in height, Scioto River) dams in 2012 and 2013, respectively. The 5th Avenue dam was constructed in 1935 in order to provide cooling water for a power plant of The Ohio State University (Figure 1.1). With the inactivity of the power plant and declining chemical water-quality conditions (US Army Corps of Engineers 2004), the dam was removed starting in August 2012. Restoration efforts took place starting in summer 2013 near The Ohio State University campus and included channel restoration at sections of a 2.6-rkm river segment. Restoration activities included reshaping the river channel, construction of in-stream habitat structures (e.g., riffles, pools), redeveloping and reconnecting floodplain wetlands, and planting riparian vegetation (see Ohio EPA 2011 for additional details).

The Main Street dam was constructed in downtown Columbus, Ohio in the late 1800’s primarily for aesthetic purposes (Figure 1.4). Dam removal proceeded in November 2013 in order to improve chemical water quality as well as increase riverfront access. Newly exposed river banks were redeveloped into publically-accessible green spaces as part of the “Scioto Greenways” project. Construction for this project included some removal of newly exposed bed material from the channel; however, other in-stream modifications did not take place.
Figure 1.4. Aerial image of the study system in downtown Columbus, Ohio (USA) including the Scioto and Olentangy Rivers. Dams within the study reaches are marked with a solid red line. Removed dams included the 5th Avenue (Olentangy River) and Main Street dams (Scioto River). Seven (500 m) study reaches near The Ohio State University campus and downtown Columbus on the Olentangy (4 study reaches) and Scioto River (3 study reaches), respectively, were used for this study. Three of these sites are associated with a previous study (Kautza & Sullivan, 2015; Kautza & Sullivan, In press; Kautza & Sullivan, In press) and represent pre-dam removal conditions. Control reaches were separated by lowhead dams and selected in order to represent upstream and downstream conditions without dam removal. Experimental reaches were selected based on different treatments: upstream/downstream of the previous dam, actively or passively restored.
5. Summary of Objectives

River ecosystems are modified by both natural and anthropogenic disturbances. Understanding the role of dam removal as an environmental disturbance has implications for fish-community dynamics and aquatic food-web structure and will provide important insights for aquatic conservation and management. However, to date, much of the research examining the consequences of dam removal for fish communities has not used a food-web approach and focused primarily on fish-assemblage structure (Kanehl et al., 1997; Catalano et al., 2007; Burroughs et al., 2010) or shifts in species distributions due to changes in dispersal or migration patterns (Burdick & Hightower, 2006; Stanley et al., 2007). Additionally, there have been few if any studies in heavily urbanized, mid-size or larger river systems (i.e., > 4th order). Thus, the overarching goal of my research was to investigate the role of lowhead dam removal as a disturbance affecting fish community dynamics. More specifically, two main objectives drove my research, each of which is addressed in a thesis chapter that has been or will be submitted for publication:

Objective 1: Investigate the short-term effects (< 2 years) of lowhead dam removal and associated restoration activities on fish assemblage structure (e.g., diversity and composition) in an urban river system. Published in River Systems, (Dorobek, Sullivan, & Kautza, 2015).

Objective 2: Quantify the influences of lowhead dam removal as a pulse disturbance with consequences for fish-centered food webs (e.g., species, link,
and connectance properties) over time (< 3 years). Target journal: *Global Change Biology* (Dorobek & Sullivan).

All animal collections performed as part of this thesis were in accordance with Institutional Animal Use and Care Protocols #2009A0215, #2009A0215-R1, 2008A0161-R1, and 2008A0161-R2; and Ohio Division of Wildlife, Wild Animal Permits #15-49 and #18-91 (Appendix A).

I anticipate that this research will provide additional information regarding the consequences of lowhead dam removal on fish community dynamics, especially in highly managed, urban river systems. Additionally, this investigation will add to our theoretical understanding of disturbance and ecological networks in rivers. Therefore, I anticipate that findings from this research will include both applied and theoretical components to further our understanding of the role of lowhead dam removal in shaping fish assemblages and food-web structure, with implications for the ecological integrity of river ecosystems.
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Chapter 2: Short-term consequences of lowhead dam removal for fish assemblages in an urban river system

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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* spp.) 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.
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 impacts 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 (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 $\leq 7.5$ m (Stanly et al., 2002), with reference to “large” dams as storage dams $> \sim 7.5$ 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 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 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) (Figure 2.1). 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, Figure 2.1). Restoration activities occurred throughout the entire restored upstream reach (OR3, Figure 1). Our upstream control reach, OR1 (Figure 2.1), 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 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 (Figure 2.1). 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” (Figure 2.1).

**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® 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 $H'$.

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

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.

\[ E = \frac{H'}{H_{\text{max}}} \] (2)

Where \( H_{\text{max}} \) 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 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 2.1).

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: $p > 0.05$) (Figure 2.2a). 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 in upstream reaches consisted of higher relative abundances of Common Carp, Smallmouth and Rock Bass (\textit{Ambloplites rupestris}), Golden Redhorse (\textit{Moxostoma erythrurum}), Brook Silverside (\textit{Lebidesthes sicculus}), Silver (\textit{Notropis photogenis}) and Golden (\textit{Notemigonous crysoleucas}) shiners, Bluntnose Minnow (\textit{Pimephales notatus}), Black Crappie (\textit{Pomoxis nigromaculatus}) and hybrid sunfish (\textit{Lepomis} spp.) (Figure 2.3a). Saugeye (\textit{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 pre-dam removal impoundments as well as the appearance and/or increased abundance of species such as Central Stoneroller (\textit{Campostoma anomalum}), Fantail Darter (\textit{Etheostoma flabellare}), and Smallmouth Buffalo (\textit{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 (Figure 2.4). Prior to dam removal, omnivorous and insectivorous species dominated the assemblages (Figure 2.4a, c, e). Following dam removal, the relative abundance of omnivores declined at OR3 with a corresponding 32% increase in the relative abundance of insectivores (Figure 2.4d). Conversely, the proportion of insectivores decreased by 20% in the upstream Scioto reach (SR1; Figure 2.4f). Note that the proportion of insectivores increased by 25% in the upstream control reach on the Olentangy River (Figure 2.4).

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 $H'$ (Figure 2.5) 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 increasing trend at the Olentangy downstream experimental reach (OR4: $t = 3.78$, $df = 2$, $p = 0.063$) [Figure 2.6a; 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 (Figure 2.6b). 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 ($p > 0.05$; Figure 2.6). $E$ 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 (Figure 2.3b). 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; Figure 2.7). The proportion of insectivores in OR3 increased by 19% such that the fish assemblage was almost entirely composed of insectivorous species (Figure 2.7f); 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 (Figure 2.7h).

**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 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) 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 (Figure 2.6), 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., 1 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 are likely to 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
5\textsuperscript{th}-6\textsuperscript{th} 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 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.
Acknowledgements

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Table 2.1. 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

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Figure 2.1. 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).
Figure 2.2. 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 $\pm 1$ standard error (SE) from the mean.
Figure 2.3. 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), SBY (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).
Figure 2.4. 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.
(a) Omnivores 47%  
Insectivores 44%  
Carnivores 8%  
Other 1%

(b) Carnivores 11%  
Insectivores 69%  
Omnivores 20%

(c) Omnivores 46%  
Insectivores 48%  
Herbivores 2%  
Piscivores 4%

(d) Omnivores 5%  
Insectivores 80%  
Carnivores 5%

(f) Carnivores 5%  
Insectivores 39%  
Omnivores 41%  
Piscivores 5%  
Herbivores 5%

(b) Carnivores 15%  
Insectivores 75%  
Omnivores 10%

(e) Carnivores 2%  
Piscivores 2%  
Omnivores 37%  
Insectivores 59%
Figure 2.5. 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.
Figure 2.6. 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.
Figure 2.7. 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.
(a) Insectivores 69%
   Omnivores 20%
   Carnivores 11%

(b) Carnivores 20%
    Omnivores 25%
    Insectivores 51%
    Piscivores 4%

(c) Insectivores 95%

(d) Insectivores 96%

(e) Insectivores 80%
    Omnivores 15%

(f) Insectivores 99%

(g) Insectivores 85%
    Omnivores 13%
    Carnivores 2%

(h) Insectivores 97%

Chapter 3: Are river food webs resilient? Changes in fish food-web structure following lowhead dam removal

Alayna C. Dorobek* and S. Mažeika P. Sullivan

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Keywords: ecological networks, disturbance, food-chain length, stable isotopes, dam removal
Abstract

Understanding how disturbance influences food-web structure and stability – a key ecological topic on both theoretical and empirical grounds – has become particularly critical given the global ubiquity of environmental perturbations. In particular, dam removal is an increasingly common environmental change with largely unknown ecological impacts. Following the removal of two lowhead dams on the Olentangy and Scioto Rivers of Columbus, Ohio (USA), we compared food-web networks characterized by species, link, chain, and web-interdependence properties over space (control and experimental reaches, upstream and downstream of previous dams, active and passive channel restoration) and time (before removal, +1-3 years following dam removal). We observed a decline in species richness across study reaches in the smaller Olentangy River, with an actively restored reach exhibiting the greatest reduction (58%) by year 3. In contrast, in the larger Scioto River, species richness exceeded pre-dam removal numbers system-wide by the end of the study. Reduced connectance and link density were most exaggerated at an actively restored reach in the Olentangy River and both upstream and downstream of the previous dam in the Scioto River, with the most pronounced loss one year following removal. These link properties had rebounded to pre-dam removal levels by the end of the study in the Scioto but not in the Olentangy River. Food-chain length (FCL) shortened by an average of 25% in Olentangy River experimental reaches, but did not change significantly in the Scioto River experimental reaches except for a significant decrease at SR1 between Y1 and Y2. FCL was significantly shorter in the Olentangy River control reach, suggesting that hydrological
and other watershed-scale features could be regulating network structure. Alterations in hydrological connectivity and ecosystem size are likely key mechanisms driving the observed changes in food-web architecture, mediated by both changes in species richness and individual traits (e.g., mean individual body size was positively related to FCL). Our results suggest that food-web networks in larger systems may be more resilient than those in smaller systems due to the capacity of wider, deeper channels to buffer against disturbance and reduce species loss. Our findings contribute to understanding the complex relationships between disturbance, ecological networks, and stability in the context of a widespread riverine change agent.

**Introduction**

Aquatic food webs are increasingly viewed as complex ecological networks (Dunne *et al.*, 2002a; Ings *et al.*, 2009) in part owing to their non-random structural patterns (e.g., modularity, nestedness) and sensitivity to indirect interactions and disturbances (Sole & Montoya, 2001; Williams *et al.*, 2002; Martinez *et al.*, 2006). Within this context, characteristics such as connectance (i.e., the proportion of realized vs. possible ecological interactions) and compartmentalization (i.e., sets of highly interacting nodes) are considered important drivers of network dynamics (May, 1972; Krause *et al.*, 2003; Poisot & Gravel, 2014). While significant theoretical advances have been made (see Dunne *et al.*, 2002), the consequences of environmental perturbations such as habitat loss, land-use change, and species invasions on food-web complexity remain unresolved. Yet, understanding the consequences of disturbance for food-web structure and, further, aquatic ecosystems are critical to our ability to manage and
preserve river ecosystem function (Romanuk et al., 2009; Thompson et al., 2012b; Cross et al., 2013).

Multiple metrics contribute to describing food-web complexity, including species, web-interdependence, chain, and link properties (Romanuk et al., 2006). Species properties include the number (i.e., species richness) and character (e.g., proportion of top predators) of taxa (Bersier et al., 2002) that relate to community and food-web structure. Changes in species richness and taxonomic composition are likely to have consequences for other food-web properties (e.g., food-chain length (FCL, see below; Post & Takimoto, 2007; McHugh et al., 2010; Sullivan et al., 2015). More specifically, shifts in species richness can affect food-web structure through the addition or removal of omnivorous or top predator species (Post & Takimoto, 2007). Additionally, species diets and trophic levels represented by feeding guilds (e.g., herbivore, omnivore, invertivore) could be important in determining food-web architecture including the number and strength of trophic interactions (Guimera et al., 2010).

Changes in species richness and composition could also affect web-interdependence properties, which could have potential implications for community dynamics and food-web structure. Beta diversity, for example, is a measure of species turnover (Whittaker, 1972) that can also be used to compare diversity and interdependence between sites (Wilson & Shmida, 1984). Shifts in species properties could also affect biotic homogenization (i.e., breakdown of regional distinctiveness of biota; Olden & Poff, 2004), which has been shown to increase with greater anthropogenic disturbance (Walters et al., 2003; Poff et al., 2007; Rahel, 2010). Homogenization of
communities includes the replacement of rare (i.e., endemic) species with narrow food and habitat requirements by tolerant non-native and widely distributed native species (i.e., cosmopolitan).

Link properties (e.g., link density, connectance) consider network complexity of food webs as mediated by the number of trophic links in relation to taxonomic richness (Bersier et al., 2002) and provide important insights to community stability in response to local species extinctions, invasions, and disturbance (Dunne et al., 2002b). Food webs with greater connectance – the ratio of the number of actual links to the number of possible links (i.e., links/species²; Bersier et al., 2002) – are usually regarded as more complex and are likely less perturbed by the loss of species (Dunne et al., 2002a; Eklof & Ebenman, 2006). The relationship between connectance and species richness has been explored theoretically (Warren, 1990; Martinez, 1992; Thompson et al., 2012b) and may aid conservation and management efforts because of its implications for trophic diversity and ecosystem processes wherein higher network connectivity promotes energy transfer and resilience to secondary extinctions (Tylianakis et al., 2007).

Chain properties consider the relative trophic positions of species in a food web (Romanuk et al., 2006). Classic food-web descriptions based on relative abundances of foraging guilds have been used to describe the approximate position, or trophic level, of species in food chains. However, assigning theoretical trophic levels to fish species can be difficult given the plasticity and seasonality of fish diets. Further, this method can underestimate the energetic importance of certain trophic interactions within the food web (Vander Zanden et al., 1997). Food-chain length, or maximum trophic position
(Vander Zanden et al., 1999; Post et al., 2000), considers the number of links between an apex predator and the base of the food web (Pimm & Lawton, 1977; Pimm & Kitching, 1987). Food-chain length via stable-isotope analysis (Vander Zanden et al., 1997; Post, 2002b) provides a quantitative measure of energetic pathways and ecological structure (Sabo et al., 2009), with evidence pointing to disturbance regime, ecosystem size and structure, and productivity as important regulatory factors (Power et al., 1996b; Post et al., 2000; Takimoto et al., 2008; McHugh et al., 2010; Sullivan et al., 2015).

Environmental perturbations can influence food-web networks in multiple ways. For example, hydrologic disturbance has been linked to FCL (Marks et al., 2000; Sabo et al., 2009), whereby unpredictable or abnormal hydrologic conditions (e.g., drought, increased streamflow variability) have been associated with shorter FCL. Because networks that are highly connected with large interaction strengths tend to be more stable (May, 1972), network structure might be expected to determine how a community responds to disturbance. However, the organization of these connections may be a more important driver of network stability than their interactions strengths (Allesina & Pascual, 2009; Stouffer & Bascompte, 2010; 2011). Highly compartmentalized trophic networks are also thought to be more stable (Krause et al., 2003) because highly connected compartments internally contain perturbations, thereby limiting cascading effects throughout the network (Stouffer & Bascompte, 2011). The mechanistic factors determining compartmentalization of food webs are not well understood, but species richness, niche organization, and life-history strategies are thought to be important (Guimera et al., 2010).
Dam removal – an increasingly widespread river restoration approach to reestablish connectivity of upstream and downstream streamflow, sediment transport, and movement of organisms (Hart et al., 2002; Doyle et al., 2003a; Gangloff, 2013) – can represent an ecologically meaningful pulse disturbance (Tullos et al., 2014; Dorobek et al., 2015). Lowhead dam (≤ 7.5 m in height; US Army Corps of Engineers, 2013) removal has been shown to have strong consequences for fish community structure (Bednarek, 2001; Doyle et al., 2005; Gardner et al., 2013). For example, increased connectivity due to dam removal has been shown to increase species richness (Hill et al., 1994; Catalano et al., 2007) and lead to a shift from lentic to lotic fish species in previously impounded habitats (Kanehl et al., 1997; Bushaw-Newton et al., 2002; Horwitz et al., 2002). Conversely, downstream sediment aggradation and habitat homogenization has shown initial declines in richness and abundance (Catalano et al., 2007; Gardner et al., 2013).

These and other community-level responses suggest that fish-centered food webs may be equally as sensitive. For instance, biotic homogenization in rivers has been driven by a lack of natural variability of streamflow regime due to dams (Poff et al., 2007; Rahel, 2007). Consequently, recovery of natural flow regimes with increased hydrologic variability due to dam removal could reestablish more sensitive riverine species reducing homogenization and further impacting food-web structure. Following the removal of two lowhead dams in Columbus, Ohio (USA), we compared food-web network properties (Table 3.1) over space (upstream and downstream of previous dams control and experimental reaches) and time (before removal, +1-3 years following dam removal).
Additionally, we compared food-web metrics in restored versus adjacent non-restored river reaches.

We hypothesized that the collective hydrogeomorphic changes following dam removal would have quantitative impacts on the network complexity of fish-centered food webs as mediated by shifts in community structure. In particular, we predicted that: (1) fish species richness would decline in the previously impounded sites and would be associated with a loss of lentic-adapted omnivorous and predatory species; (2) increased hydrological connectivity as a result of dam removal would lead to increasingly similar community composition at sites previously separated by the dams, and thus would decrease web-interdependence properties; (3) rapid hydrogeomorphic changes upstream of the dam removal (Hart et al., 2002; Doyle et al., 2003b) would have short-term consequences such as reductions in food-web connectivity (e.g., link properties would decrease initially in response to disturbance, but increased hydrologic connectivity would lead to increases in link properties over time due to an increase in species richness); (4) similarly, chain properties would shift such that the trophic position of top predators (i.e., FCL) would shorten initially in response to the rapid hydrogeomorphic changes that can occur immediately after dam removal (owing to a loss of higher trophic level species); however, FCL would likely increase over time with an increase in species richness, mean individual body size, and network connectivity.

**Experimental Approach**

**Study system and design**
We surveyed seven reaches in the Olentangy and Scioto Rivers (Columbus, Ohio) using a Before-After Control-Impact design (Stewart-Oaten et al., 1986; Kibler et al., 2011). The Olentangy River is a 5th-order tributary of the Scioto River with an average channel width of 41 m for non-impounded, experimental reaches. The Scioto River is a 6th-order system that drains into the Ohio River. The 500-m study reaches were distributed both upstream and downstream of lowhead dams that were removed in 2012 (5th Avenue Dam, 2.5 m high, Olentangy River) and 2013 (Main Street Dam, 4.1 m high, Scioto River) (Figure 3.1). The 5th-Avenue dam, which previously served as a source of cooling water for a now inactive power plant of The Ohio State University, was removed in order to improve water quality and aquatic habitat (US Army Corps of Engineers, 2004). Active channel restoration efforts took place after the removal (summer through fall 2013) and included reshaping and developing a 2.6-km upstream river segment, redeveloping and reconnecting floodplain wetlands, and planting riparian vegetation (see Ohio EPA, 2011 for additional details). An additional upstream portion was left to passively restore (OR2, Figure 3.1).

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 19th century largely for aesthetic purposes and removed in November 2013 to improve water quality, habitat, and increase riverfront access. In-stream channel restoration did not take place after the removal of this dam; however, newly exposed riverbanks were reestablished and reconstructed from remaining substrate to develop publically accessible green space. The downstream control reach, SR3 was located downstream of the 3.4-m high run-of-river
Greenlawn Avenue dam (Figure 3.1). We assigned several treatments to our study reaches (e.g., upstream/downstream of dams, actively/passively restored sections, before/after) to assess the impacts of dam removal and subsequent restoration activities on food-web properties. For clarity, control reaches are designated as “upstream control” and “downstream control.” Control reaches were separated by lowhead dams and represented both impounded (OR1) and free-flowing (SR3) conditions. All others are designated as “experimental reaches” (Figure 3.1).

**Biotic sampling**

*Fish surveys*

We conducted fish surveys from 2011 to 2015 during the stable, baseflow period of late summer-early autumn. OR1 and SR3 (upstream and downstream controls, respectively) as well as experimental reaches OR3, SR1, and SR2 were sampled prior to dam removal. We sampled all reaches once per year for two years following dam removal on the Scioto River and for three years following dam removal on the Olentangy River. Each reach was stratified into bottom, middle, and top sections and then each of these sections by right bank, mid-channel, and left bank transects (running longitudinally, upstream to downstream within each section). We sampled 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® boat unit. The type of sampling unit we used depended on the physical characteristics (e.g., depth, conductivity) of the study reach. Sampling effort was based on a pre-dam removal effort of 600 s per transect (total of
5,400 s per reach). We adjusted our sampling effort with changes in the sampling unit associated with changes in habitat volume and complexity in accordance with other dam removal studies (McLaughlin et al., 2006; Catalano et al., 2007, Maloney et al., 2008) by reducing time spent sampling at each transect with reductions in habitat volume.

We dispatched 3-5 individuals on ice from the most common fish species representing major trophic guilds (Table 3.3) for stable-isotope analysis. We transported specimens on ice to the laboratory where they were kept frozen until processing. In the laboratory, we removed plugs of skinless dorsal muscle tissue (Pinnegar & Polunin, 1999), dried by sublimation using a freeze dryer for 48-72 hours, and packed in tin capsules for subsequent $^{13}$C and $^{15}$N stable-isotope analysis.

**Basal resources**

We collected periphyton (i.e., benthic algae) during the summer months (June-August; once per summer) at all study reaches. We brushed periphyton (using a toothbrush) from the surface of ~10 benthic substrate particles (e.g., large gravel, cobble, and rocks) from downstream, middle, and upstream portions of each reach. Periphyton was rinsed into an opaque plastic sample jar (Finlay et al., 1999) and stored in a cool environment in the laboratory. All animal material, non-algal detrital material, and filamentous macroalgae were removed from the samples that were then dried for 48 h at 60°C and packed in tin capsules for stable-isotope analysis (Lorrain et al., 2003).

We collected terrestrial detritus (e.g., leaves from riverbank trees and shrubs) using six floating pan traps positioned on the edge of the river channel and distributed
equidistantly along the entire length of the reach. We set pan traps for one, 10-day period during each summer (June-August). In the laboratory, leaves were cleaned of any non-plant material, dried for 48 h at 60°C, and ground into a fine powder using a ball mill grinder. After grinding, powdered detritus was packed in tin capsules for stable-isotope analysis.

**Food-web properties**

*Species properties*

From our fish surveys, we determined species properties (species richness; relative abundances of top predator, intermediate, and basal species) for each transect (bottom, middle, top) at each reach. Species richness included only fishes and not other basal taxa in the food web (e.g., mollusks, aquatic insects). Trophic levels of fishes were based on fish-centered food webs (i.e., fish as consumers). Fishes were classified as top predators if they have prey but no consumers, intermediate if they have prey and consumers, and basal if they only have consumers following Kautza and Sullivan (In press) (see Supporting Information: Table 3.3 for additional details).

*Web-interdependence properties*

We calculated web-interdependence properties for each individual transect (homogenization) or the entire reach (beta diversity). We used the Sørensen index ($\beta_{sor}$) to measure beta diversity at each reach. $\beta_{sor}$ is a measure of similarity that incorporates presence and absence data of species in a community:
\[ \beta_{\text{Sor}} = \frac{2a}{2a + b + c} \]  

where “a” is the number of species shared between two communities and the number of species unique to each community are “b” and “c”, respectively (Oksanen et al., 2016). With similarity indices, a larger \( \beta_{\text{Sor}} \) indicates less species turnover.

We calculated the ratio of endemic to cosmopolitan species richness (Er:Cr) and abundance (Ea:Ca) for each reach to generate a reach-wide mean as a measure of homogenization where a ratio > 1 indicates the presence of more endemic species or individuals (Walters et al., 2003). For the purposes of this study, species were classified as endemic or cosmopolitan based on state and national distributions (Becker, 1983), habitat preferences, and Ohio Environmental Protection Agency’s (EPA) tolerance listing (e.g., rare, sensitive, tolerant; Ohio EPA, 2014; see Appendix C). Therefore, cosmopolitan species included tolerant natives with large distributions as well as non-native fish species (Rahel, 2010).

**Chain properties**

The use of stable-isotope techniques to measure FCL has been adopted to provide a more quantitative approach to describe food-web structure (Rounick & Hicks; Post, 2002a; Thompson et al., 2012b). Conversely, a theoretical approach to constructing FCL has been shown to underestimate food-web complexity (Gladyshev, 2009; Lau et al., 2009). All samples (e.g., detritus, periphyton, fish) were analyzed for \(^{13}\)C and \(^{15}\)N by continuous flow isotope ratio mass spectrometry (Delta Plus XP, Termofinnigan, Bremen, Germany) at the Washington State University Stable Isotope Core (Pullman,
Washington). Stable-isotopes ratios are reported in δ notation as parts per thousand (‰) deviation from an established standard (e.g., Pee Dee belemnite limestone for δ¹³C; atmospheric N for δ¹⁵N).

\[
\delta^{13}C \text{ or } \delta^{15}N = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000
\]

where \( R = ^{13}C/^{12}C \) or \(^{15}N/^{14}N\).

We used δ¹³C and δ¹⁵N values to estimate trophic position (TP) of fishes and FCL of fish food webs [estimated as the maximum TP at each reach (Cabanna & Rasmussen, 1996; Vander Zanden & Rasmussen, 1999)]:

\[
\text{TP} = \lambda + (\delta^{15}N_{\text{consumer}} - [\delta^{15}N_{\text{base1}} \times \alpha + \delta^{15}N_{\text{base2}} \times (1 - \alpha)])/\Delta_n
\]

where \( \lambda = \text{TP of the baseline (i.e., TP = 1 for the primary producers we used as the baselines); } \alpha = \text{the proportion of N acquired from baseline one (i.e., terrestrial detritus); } \) and \( \Delta_n = \text{fractionation rate of N, commonly considered as a } 3.4 \text{ ‰ increase per trophic level (Post 2002); however, other estimates could be used (e.g., 2.54 ‰; see Vanderklift & Ponsard, 2003). Additionally, 0.4 ‰ serves as the commonly used enrichment value for C. Following the assumption that C and N move through the food web similarly, a simple 2-end member linear mixing model is sufficient to estimate } \alpha:

\[
\alpha = (\delta^{13}C_{\text{consumer}} - \delta^{13}C_{\text{base2}})/(\delta^{13}C_{\text{base1}} - \delta^{13}C_{\text{base2}})
\]

We used terrestrial detritus (\( \delta^{13}C_{\text{base1}} \)) and periphyton (\( \delta^{13}C_{\text{base2}} \)) as our reach-specific baselines given that they were collected during a similar time period as aquatic food-web consumers (i.e., fish; Post, 2002b).
Link properties

In order to determine link properties (i.e., connectance, link density), we constructed a predator-prey binary matrix for each transect at each reach that described “fish-centered” networks following (Winemiller, 1990; Romanuk et al., 2006). Fish-centered food webs included all fish species sampled at each reach as well as lower trophic taxa and basal resources commonly present in mid-size river systems that we aggregated into larger taxonomic groups (e.g., aquatic insects, crustaceans, zooplankton, mollusks, small fish, detritus, plants, algae) similar to Romanuk et al. (2006). Species diets were determined from a review of the literature (Trautman, 1981; Becker, 1983).

We used the predator-prey matrix to determine the number of theoretical trophic interactions, or links, in order to calculate connectance and link density. Link density was measured by dividing the number of links by species richness ($L/S$). We used $L/S^2$ – number of links divided by the total possible links- as a measure of connectance (i.e., directed connectance; Bersier et al., 2002).

Statistical Methods

All data were transformed where necessary to meet assumptions of normality and homogeneity of variance. We used linear mixed models to assess potential differences in our response variables (see food-web properties outlined in Table 3.1) among reaches (representing control, upstream/downstream, actively restored/passively restored treatments) and time for (1) “after” dam removal data for all Olentangy River reaches and (2) all Scioto reaches and time steps. Time, reach, and a reach-time interaction were
included as fixed effects with transects nested within study reaches included as a random effect. Because we only had “before” data for the upstream control (OR1) and upstream actively restored (OR3) reaches, we were not able to include all Olentangy River time steps and reaches in one model. Instead, we used paired t-tests to evaluate potential differences in our response variables between before and after (year 1-3) dam removal at OR1 and OR3. We used linear and non-linear regressions to explore potential proximate mechanisms associated with food-web structure (number of links, FCL) including species richness, link density, connectance, and mean fish body length. We used JMP 12.0 (SAS Institute, Cary, North Carolina) for all statistical tests. We used \( \alpha \leq 0.05 \) to indicate statistical significance, with \( \alpha \leq 0.10 \) as evidence of a trend (e.g., Rowse et al. 2014).

**Results**

*Species Properties*

A total of 4,663 individual fish were sampled across the seven study reaches, representing 60 species. For the Olentangy River, mean species richness ranged from 17.3 (OR1) to 23 (OR3) before dam removal and 4.3 (OR3) to 14.3 (OR1) following dam removal. For the Scioto River, mean species richness ranged from 12 (SR1) to 17 (SR2) before dam removal and 5 (SR1) to 22 (SR3) following dam removal. Species richness after dam removal was not significantly different than before dam removal in the upstream Olentangy River control reach (OR1, paired t-test: \( t = -3.67, df = 2, p = 0.067 \); Figure 3.2a). Likewise, removal of the Main Street dam in the Scioto River did not prompt a significant shift in species richness at the downstream control reach (SR3, linear
mixed model: $p = 0.130$, Figure 3.2b). Mean species richness for all Olentangy River experimental reaches increased over time (linear mixed model: $p = 0.002$; Table 3.2) in the years following removal (Tukey’s HSD: Y2, $p = 0.002$; Y3, $p = 0.017$; Figure 3.2a). However, species richness at the actively restored experimental reach (OR3) had not returned to pre-dam removal conditions ($S = 23$) by Y3 ($S = 14$) (paired t-test: $t = -6.42$, $df = 2$, $p = 0.023$; Figure 3.2a). In contrast, species richness changed over time (linear mixed model: $p < 0.0001$; Table 3.2) with a significant increase between Y1 and Y2 at both Scioto River experimental reaches: SR1 (Tukey’s HSD: $p = 0.002$) and SR2 (Tukey’s HSD: $p = 0.040$). However, species richness was also greater at the downstream Scioto River control reach (Tukey’s HSD: $p > 0.05$), suggesting watershed-scale factors may also be at play.

We also observed differences among study reaches/treatments. In the Olentangy River, there were considerable differences in mean species richness among reaches in the first year following dam removal (linear mixed model: $p = 0.002$; Table 3.2), but no differences among reaches were observed by Y2 and Y3 (Tukey’s HSD: $p > 0.05$; Figure 3.3a). For instance, the passively restored reach (OR2) exhibited greater species richness than the actively restored reach (OR3) in Y1, but not in Y2 or Y3. We observed no differences in species richness among Scioto River reaches before dam removal (Tukey’s HSD: $p > 0.05$), the greatest species richness at the downstream control reach (SR3) in Y2 (Tukey’s HSD: $p = 0.015$), and no differences in Y3 (Tukey’s HSD: $p > 0.05$; Figure 3.4a).

No top predators were sampled at the Olentangy River reaches before or after
dam removal. In the Scioto River, the relative abundance of top predators did not vary significantly among reaches (linear mixed model: $p = 0.163$; Table 3.2) or over time (linear mixed model: $p = 0.071$; Table 3.2). Intermediate species – defined as species with both fish predators and prey – represented a small proportion of the total fish abundance across the study reaches and were dominated by Smallmouth Bass ($Micropterus dolomieu$; 3.8%), Largemouth Bass ($Micropterus salmoides$; 1.5%), and Freshwater Drum ($Aplodinotus grunniens$; 0.7%) (see Supporting Information: Table 3.3). The relative abundance of intermediate species did not change over time following dam removal at the upstream Olentangy River control reach (OR1, paired $t$-test: $t = 1.94$, $df = 2$, $p = 0.192$; linear mixed model: $p = 0.051$; Table 3.2, Figure 3.2c) however, relative abundance of intermediate species for Olentangy River experimental reaches increased significantly between Y1 and Y3 (linear mixed model: $p = 0.013$; Table 3.2, Figure 3.2b). The relative abundance of intermediate species did not vary by time or reach for the Scioto River control or experimental reaches (linear mixed models: $p > 0.05$; Table 3.2, Figure 3.4d).

Basal species composition varied between reaches and years and included sunfish ($Lepomis$ spp.), darters ($Etheostoma$ spp. and $Percina caprodes$), and various suckers and cyprinids including Bluntnose Minnow ($Pimephales notatus$) and Common Carp ($Cyprinus carpio$) (see Supporting Information: Table S1). The relative abundance of basal species did not change over time or vary among reaches in the Olentangy River following dam removal (linear mixed models: $p > 0.05$; Table 3.2, Figures 3.2e, 3.3c). However, the relative abundance of basal species increased by 8% in Y2 at the upstream
actively restored reach (OR3) compared to pre-dam removal levels (paired $t$-test: $t = 5.37$, $df = 2$, $p = 0.033$; Figure 3.2e). Whereas the Olentangy River control reach exhibited no change compared to pre-dam removal measures (OR1, paired $t$-test: $t = 5.37$, $df = 2$, $p = 0.033$; Figure 3.2e), the relative abundance of basal species increased by 39% over time at the downstream control reach on the Scioto River (SR3, Tukey’s HSD: S3-Y1, $p = 0.016$; Y2, $p = 0.009$, Figure 3.2f). The interaction of reach and time also emerged as a significant influence on the relative abundnance of basal species in the Scioto River (linear mixed model: $p = 0.002$; Table 3.2).

**Web-Interdependence Properties**

Homogenization metrics did not vary significantly in the Olentangy River control reach after dam removal (OR1, paired $t$-test: Er:Cr – $t = 2.97$, $df = 2$, $p = 0.097$; Ea:Ca – $t = 3.00$, $df = 2$, $p = 0.096$, Figure 3.5a,c); however Ea:Ca decreased over time (linear mixed model: $p = 0.024$; Table 3.2) at the Scioto River control reach (SR3, Tukey’s HSD: $p = 0.043$; Figure 3.5b). Er:Cr nearly doubled by Y2 at OR3 compared to pre-dam removal levels (paired $t$-test: $t = 5.40$, $df = 2$, $p = 0.033$; Figure 3.5c). Homogenization did not change in the years following dam removal in the Olentangy (Figure 3.5a,c) or Scioto (Figure 3.5 b,d) River experimental reaches (Table 3.2). However homogenization decreased over time at the passively restored reach (OR2,) where Ea:Ca decreased by 64% in Y3 (linear mixed model: $p = 0.0006$; Tukey’s HSD: Y2, $p = 0.001$; Y3, $p = 0.001$; Table 3.2, Figure 3.5a). Homogenization varied among Oletangy River experimental reaches after dam removal (OR2-4, linear mixed models: Ea:Ca, $p = 0.019$; Er:Cr, $p =$
0.017; Table 3.2). More specifically, OR2 was less homogenized than the other Olentangy River experimental reaches, particularly in the first year following dam removal (linear mixed model: \( p = 0.0006 \), Table 3.2). Ea:Ca was 746 and 229% greater at OR2 than at OR3 (Tukey’s HSD: \( p = 0.0005 \)) and OR4 (Tukey’s HSD: \( p = 0.0007 \)), respectively in the first year after dam removal. In the Scioto River, homogenization varied between the control (SR3) and the experimental reaches (SR1-2) (Ea:Ca, linear mixed model: \( p = 0.03 \); Table 3.2) where SR3 had a significantly larger Ea:Ca than SR1 and SR2 (Tukey’s HSD: \( p = 0.003, p = 0.011 \), respectively) prior to dam removal.

In general, beta diversity decreased over time within and among reaches as represented by an increasing Sørensen index (Figure 3.6). Beta diversity did not change substantially at the upstream Olentangy River control reach (OR1) ranging from 0.61 (Y1-Y2) to 0.67 (Y2-Y3) or the passively restored reach (OR2) ranging from 0.61 (Y1-Y2) to 0.64 (Y2-Y3). However, beta diversity decreased at the actively restored reach (OR3) and the downstream (OR4) Olentangy River reaches with fish communities becoming more similar over time. Additionally, community composition at OR2 and OR3 converged over time [0.52 (Y1) to 0.87 (Y2) to 0.68 (Y3)] (Figure 3.6a). Sørensen index also increased between SR2 and SR3 [0.62 (Before) – 0.80 (Y2)] over time. The upstream experimental reach on the Scioto River (SR1) experienced the greatest species turnover thru time (0.39-0.41; Figure 3.6b).

*Link Properties*

Link properties showed a decreasing trend in response to dam removal in the
Olentangy River control reach (OR1, paired $t$-test: connectance – $t$ = 3.65, $df$ = 2, $p$ = 0.068; link density – $t$ = -0.09, $df$ = 2, $p$ = 0.935; Figure 3.7 a,c) but were statistically invariant in the Scioto River control reach (SR3, linear mixed models: connectance – $p$ = 0.185; link density – $p$ = 0.01; Figure 3.7b,d). Whereas connectance did not vary over time after dam removal for the Olentangy reaches (linear mixed model: $p$ > 0.05; Table 3.2; Figure 3.7a), mean connectance for all Scioto reaches decreased significantly in Y1 following dam removal (linear mixed model: $p$ = 0.005; Table 3.2, Figure 3.7b).

Similarly, connectance and link density decreased by 38 and 65%, respectively, following dam removal at the Olentangy River upstream actively restored reach (OR3, paired $t$-test: connectance – $t$ = -6.46, $df$ = 2, $p$ = 0.023; link density – $t$ = -13.54, $df$ = 2, $p$ = 0.005, Figure 3.7a, c) and was significantly lower than pre-dam removal measures over time (paired $t$-test: $p$ < 0.05). Mean link density changed over time for the Scioto River experimental reaches (linear mixed model: $p$ < 0.0001; Table 3.2), with an initial decrease at both experimental reaches (Tukey’s HSD: SR1, $p$ = 0.008; SR2, $p$ < 0.001) followed by an increase in Y2 (Tukey’s HSD: SR1, $p$ < 0.0001; SR2, $p$ = 0.0005; Figure 3.7d).

Connectance and link density varied between experimental and control reaches in the Olentangy River (linear mixed models: connectance – $p$ = 0.006; link density – $p$ = 0.002; Table 3.2). In general, mean connectance and link density were significantly lower than the control reach (OR1) in Y1 (Figure 3.8a,c). Mean connectance did not vary between any of the Scioto River reaches (linear mixed model: $p$ = 0.838; Figure 3.8b); however, link density was significantly higher (Table 3.2) in the downstream control
reach (SR3) than the upstream experimental reach (SR1) in Y1 (Tukey’s HSD: \( p = 0.017 \); Figure 3.8d). There was a strong positive linear relationship between species richness and the number of links (\( R^2 = 0.952 \), \( F = 1323.24 \), \( p < 0.0001 \); see Supplementary Figure 3.13); non-linear models did not result in a stronger relationship (data not shown).

**Chain Properties**

Prior to dam removal, mean FCL was lowest at OR1 (3.08) followed by SR3 (3.53) and OR3 (4.37). After dam removal, FCL ranged from 2.43 (OR1) to 3.89 (OR2) over three years in the Olentangy River and 2.92 (SR1) to 4.38 (SR2) over two years in the Scioto River. The highest trophic positions before dam removal were occupied by predators including Smallmouth and Largemouth Bass, and Longnose Gar (*Lepisosteus osseus*; Scioto River only). Following dam removal in the Olentangy River, the highest trophic positions were occupied by smaller-bodied insectivores including Logperch (*Percina caprodes*), Greenside Darter (*Etheostoma blennoides*), Green Sunfish (*Lepomis cyanellus*), and Johnny Darter (*Etheostoma nigrum*).

Although FCL did not change significantly between before and after dam removal in the Scioto River control reach (SR3, paired \( t \)-test: \( t = 3.43 \), \( df = 2 \), \( p = 0.076 \); Figure 3.9b), FCL decreased by almost one unit between Y1 and Y2 following dam removal in the Olentangy River control reach (OR1, linear mixed model: \( p = 0.003 \); Tukey’s HSD: \( p = 0.046 \); Table 3.2, Figure 3.9a). FCL decreased in the year following dam removal and by an even greater extent (36%) at the actively restored reach (OR3, paired \( t \)-test: \( t = -12.51 \), \( df = 2 \), \( p = 0.006 \)) and had not returned to pre-dam removal levels by Y3 (paired \( t \)-
test: $t = -30.56, df = 2, p = 0.001$; Figure 3.9a). FCL also decreased significantly in Y2 (Tukey’s HSD: $p = 0.039$; Figure 3.9a) and Y3 (Tukey’s HSD: $p = 0.043$) in the Olentangy River upstream passively restored reach (OR2) compared to Y1. A similar decline occurred between Y1 and Y2 at the upstream Scioto River reach (SR1, linear mixed model: $p = 0.001$; Tukey’s HSD: $p = 0.0004$; Figure 3.9b). However, the downstream experimental and control reaches (Scioto River) did not experience shifts in FCL following dam removal (linear mixed model: $p > 0.05$, Table 3.2). Mean FCL was significantly lower in OR3 than in OR1 and OR2 in Y1, but no differences were observed by Y2 (linear mixed model: $p = 0.0002$; Table 3.2, Figure 3.10a). In the Scioto River, mean FCL was consistent across study reaches in Y1 but significantly lower in SR1 compared to SR2 and SR3 by Y3 (linear mixed model: $p = 0.0002$; Table 3.2, Figure 3.10b). Connectance ($R^2 = 0.293, F = 22.74, p < 0.0001$; Figure 3.12) and mean fish body length ($R^2 = 0.221, F = 4.81, p < 0.043$; Figure 3.11) were positively related to FCL, with non-linear models not resulting in stronger relationships (data not shown).

**Discussion**

Dams have been constructed for thousands of years for myriad purposes including navigation, flood control, hydropower generation, and water supply for agriculture and human consumption (WCD, 2000). The last 60 years have witnessed an increase in the number and storage of dams and impoundments, with smaller reservoirs widely distributed across the globe and likely exerting strong influences on the spatial extent of flow alterations (Downing et al., 2006, Lehner et al., 2011). At the same time, dam
removal has become increasingly common as dams become ineffective, unsafe, or filled with sediment (reviewed in O’Connor et al., 2015).

Here, we present findings related to the ecological consequences of dam removal, which represents a significant, yet poorly understood, global change. Alterations in characteristics of fish-centered food webs such as species richness, connectance, link density, and food-chain length – many of which were observed by the first year following removal – suggest that lowhead dam removal acts a pulse disturbance that can affect food-web dynamics in multiple ways. In the Scioto River system, initial losses in food-web complexity largely rebounded by two years following dam removal, whereas in the Olentangy River pre-dam-removal levels were commonly not attained by year three suggesting that food-web networks in larger systems may be more resilient to dam-removal disturbance. Trophic interactions among species in a community are central to understanding ecosystem processes (e.g., nutrient cycling, transfer of aquatic contaminants; e.g., Sullivan & Rodewald, 2012) and community stability (Deangelis, 1975; Sole & Montoya, 2001; Dunne et al., 2005). Thus, our results have theoretical implications relative to the environmental drivers of network complexity, as well as applied implications relative to global patterns of river ecosystem resilience.

Species properties

Consistent with our first hypothesis, species richness declined in the previously impounded reach in the Olentangy River (OR3) immediately after dam removal (Y1; Figure 3.2a). Furthermore, species richness did not return to pre-dam removal numbers
by the end of the study in the Olentangy River but had exceeded pre-dam removal values in the Scioto River (Figure 3.2b). Responses of fish assemblage structure to lowhead-dam removal can range from several months to decades (Hart et al., 2002; Hart & Poff, 2002; Doyle et al., 2005). A decrease in species richness shortly after dam removal (e.g., OR3) would suggest a rapid response to disturbance; yet, fish-assemblage structure could continue to shift over time (e.g., SR1, SR2). Species richness typically increases with ecosystem size in fluvial systems (Angermeier & Schlosser, 1989; McHugh et al., 2010).

Dam removal and associated restoration activities led to substantial upstream reductions in channel width likely contributing to reduced species richness owing to reduced habitat availability (Sabo et al., 2010). At OR3, channel width decreased by approximately 40 m following dam removal (85 to 42 m). The channel width at the upstream Scioto River reach (SR1) also decreased after dam removal (155 to 95 m); however, channel width at this reach was still approximately twice the size of the Olentangy River experimental reaches following dam removal. Larger river systems with associated larger channel widths are likely to sustain greater species richness and could further explain why species richness returned to pre-dam removal levels after initial declines in the Scioto River.

The upstream Olentangy River passively restored reach (OR2) supported greater species richness than the actively restored reach (OR3) in the year following dam removal (Figure 3.3a), presumably at least partly as a consequence of active channel engineering that limited species colonization (Burroughs et al., 2010; Kornis et al., 2015). Although active restoration efforts did not enhance species richness during the course of the study, longer-term monitoring efforts will be necessary to determine the
efficacy of channel restoration efforts associated with lowhead dam removal. Significant
shifts in species richness were not associated with changes in the relative abundance of
intermediate or basal species; however, a significant increase in species richness in Y3
was accompanied by an increase in intermediate species at the Olentangy River
experimental reaches (Figure 3.2c). Additionally, Dorobek et al. (2015) found substantial
shifts in community composition at these reaches between Y1 and Y2. Even further, a
significant shift in community composition occurred after dam removal at the upstream,
impounded reaches. Changes in community composition were supported by marked
shifts in functional feeding groups (i.e., insectivores, invertivores, piscivores; Dorobek et
al., 2015, Table 3.3). Yet, changes in basal and intermediate species did not reflect these
changes.

Connectance and link density

Theory suggests that complex ecological networks may be “fragile” in multiple
ways. For instance, because every species is tightly linked to every other species
(Montoya & Solé 2002), impacts to one species should propagate through the network.
Link density decreased as an immediate response to dam removal yet increased over time
after Y1 at both Olentangy (OR3 only; Figure 3.7c) and Scioto (Figure 3.7d) River
experimental reaches. Additionally, connectance showed a similar decline in Y1 at OR3
(Figure 3.7a). Connectance and link density did not return to pre-dam removal levels at
the Olentangy River experimental reaches, but had largely returned to pre-dam removal
levels by Y2 in the Scioto River (Figure 3.7). Additionally, species richness was
positively related to the number of links within the food web (Supplementary Figure 3.13), consistent with results from Dunne (2004). We interpret these results as evidence that disturbances from both dam removal and the active channel restoration, which were also associated with depressed species richness, removed highly-connected species (Cohen & Briand, 1984; Paine, 1988; Warren, 1990; Murtaugh & Kollath, 1997), thereby lowering connectance and link density and at least theoretically decreasing community stability (Dunne et al. 2002b). However, the scale of the relationship between species richness and connectivity is highly contested (Winemiller, 1989; Schmid-Araya et al., 2002), and more likely dependent on changes in “trophic” species (Martinez, 1991) versus actual species richness (Winemiller, 1990; Martinez, 1992; Dunne et al., 2002b). Again, ecosystem size may be a primary mechanism, wherein the narrower Olentangy River reaches only supported few predatory and large-bodied in the years following dam removal (Dorobek et al., 2015), while largely invariant channel widths in the Scioto River following dam removal were associated with minor losses in “trophic” species and less fragile ecological networks.

In streams, connectance has been shown to be linked to habitat heterogeneity and flow disturbance; Schmid-Araya et al. (2002) postulated that lower connectance was inversely related to habitat heterogeneity (Keitt, 1997), which limits the number of encounters and, therefore, trophic interactions between species. It is possible that our literature-based trophic link estimates and aggregation of lower trophic taxa (e.g., zooplankton, aquatic insects) were not sufficiently resolute to capture the frequency and character of trophic interactions. Yet, our values of link properties fell into the range of
previous studies (Romanuk et al., 2006). Further, connectance values were similar to the universal mean connectance value (i.e., 0.11) proposed by Martinez (1992). Other investigations have claimed that life-history patterns and colonization dynamics could be important factors controlling network complexity (Parker & Huryn, 2013). Increased hydrological connectivity between the Olentangy River reaches could explain the increase in link properties over time after dam removal at the Olentangy River experimental reaches. Additionally, shifts in community composition and functional feeding groups observed by Dorobek et al. (2015) could contribute to these patterns.

**Food-chain length**

Our estimates of FCL, ranging from 2.43 to 4.38, were on par with that other food-web studies using fish as top predators in aquatic systems (e.g., 3.74-4.52, Vander Zanden et al., 1999; 2.60-4.40, but not that this estimate also included waterbirds, Sullivan et al., 2015). Food-chain length decreased significantly in response to dam removal at the upstream, actively-restored reach (OR3; Figure 3.9a). In line with other food-web properties, FCL did not return to pre-dam removal levels on the Olentangy River. Following dam removal, there was a notable shift in the functional role of species at the Olentangy River experimental reaches that occupied the maximum trophic position at this reach where top trophic positions were occupied by smaller-bodied insectivores (See Supplementary Table 3.3; Dorobek et al., 2015). Several investigators have explored the relationship between ecosystem size and FCL in stream and river ecosystems (Thompson & Townsend, 2005; Vander Zanden & Fetzer, 2007; McHugh et al., 2010;
Sullivan et al., 2015). Removal of top predators, for instance, can serve as a proximate mechanism regulating FCL (Post & Takimoto, 2007), and likely explains the > 1 decrease in trophic position observed at this site. Estimates of FCL from a study by Kautza & Sullivan (In press) in the same system were typically higher (ranging from 3.66 to 4.35), and the maximum trophic position was occupied by higher-level taxa including Largemouth Bass, Smallmouth Bass, and Flathead Catfish, suggesting that the removal of these species (especially adult Micropterus spp.) at OR3 shortened FCL. Although we observed shorter food chains in Olentangy River free-flowing reaches after dam removal, findings by Kautza and Sullivan (In press) – who found that impounded reaches typically supported shorter FCL than free-flowing reaches – suggest that FCL may lengthen in time. FCL in the Scioto experimental reaches did not change significantly (except declines at SR1; Figure 3.9b).

In addition to a significant decline in FCL in the year following dam removal, FCL continued to change over time after dam removal for some reaches. Unlike other food-web properties and contradicting our predictions, FCL decreased at the upstream Olentangy River control (OR1) and passively restored (OR2) reaches in the 2\textsuperscript{nd} and 3\textsuperscript{rd} years after dam removal (Figure 3.9a), and the downstream Scioto River control reach (SR3; Figure 3.9b), indicating that system-wide factors also likely constrain FCL. Inter-annual variation in primary production can regulate FCL (Jenkins et al., 1992; Marks et al., 2000; Takimoto et al., 2012; Parker & Huryn, 2013). Additionally, increased hydrological connectivity between reaches might be expected to influence the movement of species from different trophic guilds, especially omnivorous or top predator species.
(Post & Takimoto, 2007; Warfe et al., 2013). However, intact lowhead dams separate OR1 from downstream experimental reaches and SR3 from upstream experimental reaches, and thus this mechanism is unlikely to explain FLC-changes in these reaches. However, there was substantial hydrologic variability over the course of this study (see Supplementary Figure 3.13). While spring-early summer months experienced higher flow events, the timing and magnitude of these events were variable. For example, high flows peaked in June 2013 for both rivers whereas in 2014 (but note that these peaks were still below the 2-yr flood recurrence interval), rivers were near baseflow conditions during in June. Annual mean discharge was also substantially lower in 2015 for both the Olentangy and Scioto Rivers. Discharge has been shown to be an important driver of FCL (Marks et al., 2000; Parker & Huryn, 2006; McHugh et al., 2010, Sabo et al., 2010) suggesting that FCL was likely influenced by broad-scale hydrologic patterns in our study. Yet, the role of discharge in regulating FCL is inconclusive to date and likely dependent on multiple factors including the ranges of discharge (Walters & Post, 2008).

To observe potential proximate mechanisms driving shifts in FCL, we explored the relationship between mean body length and FCL. Predators typically are larger than their prey (Cohen, 2007) suggesting that a larger body size would be associated with higher trophic positions. We observed a positive relationship between mean body length and FCL (Figure 3.11). Further, larger fish species and top predators [e.g., Muskellunge (Esox masquinongy), Longnose Gar (Lepisosteus osseus), Flathead Catfish (Pylodictis olivaris)] were associated with impounded and Scioto River reaches. Other investigations have found that larger habitats tend to support larger organisms and longer food chains.
(Power, 2002). Moreover, larger ecosystems have been shown to absorb the effects of disturbance and, resultantly, enhance environmental stability and support longer food chains (Sabo et al., 2010). Thus, individual species traits may be an important mediator between the ecosystem size and food-web structure. We anticipate that consideration of additional traits (e.g., behavioral, dispersal, etc.) will be of considerable benefit in further understanding proximate mechanisms of network structure.

*Web interdependence*

Whereas homogenization metrics were not highly variable for the Olentangy or Scioto Rivers, important patterns emerged. In general, endemic species were typical of pool-riffle, gravel-bed river systems including either large, free-flowing river [e.g., Smallmouth Buffalo (*Ictobius bubalus*), Freshwater Drum (*Aplodinotus grunniens*)] or riffle [e.g., River Redhorse (*Moxostoma carinatum*), *Etheostoma* spp.] species. The ratio of endemic to cosmopolitan species richness increased significantly in the 2nd year after dam removal in the Olentangy River actively restored reach (OR3), and corresponded with the reestablishment of lotic-adapted species including several *Etheostoma* species including Banded (*Etheostoma zonale*), Jonny (*Etheostoma nigrum*) and Fantail (*Etheostoma flabellare*) Darters. An increase in lotic species has been associated with previous dam removal studies (Bushaw-Newton et al., 2002; Catalano et al., 2007; Maloney et al., 2008). Although endemic species richness increased at OR3 in Y2, the passively restored OR2 exhibiteded significantly declines in endemic species abundance (Figure 3.5a). Fish community structure in both rivers converged over time (decreased
beta diversity) suggesting enhanced connectivity due to dam removal, which is in line with other dam removal studies (Maloney et al., 2008; Burroughs et al., 2010; Gardner et al., 2013; Hogg et al., 2015). Increased connectivity between experimental reaches and changes in hydrogeomorphic characteristics associated with dam removal (Pizzuto, 2002; Doyle et al., 2003b; Burroughs et al., 2009) might have driven homogenization patterns at these reaches. Yet, broader landscape features could also limit the distribution of endemic species. Urbanization has been associated with decreased fish diversity and abundance and lowered index of biotic integrity (IBI) scores (Wang et al., 2000; Wang et al., 2001). Even further, fish assemblages tend to be more homogenized in urban river systems (Walters et al., 2003), which could have further implications for food-web structure. The urban influence – on this and other food-web properties – is an important consideration given the increasing urban global footprint (increase of 3.8 to 6.4 billion by 2050; United Nations, 2014), and the multiple stressors that urban streams experience (e.g., urban stream syndrome; Paul and Meyer, 2001). Because urban landscapes might be expected to constrain ecosystem recovery after dam removal, evaluating dam removal in less-managed systems may yield different results.

**Food-web stability**

Theoretically, compartmentalization increases stability in ecological networks (Krause et al., 2003) by reducing the impacts of disturbance (by retaining the effects of perturbations within strongly connected sub-groups; Stouffer & Bascompte, 2011) and thereby providing a mechanism by which complexity can persist. Furthermore, the
removal of highly-connected species can lead to higher rates of secondary extinctions than the removal of random, less-connected species, which has further consequences for food-web structure and stability (Sole & Montoya, 2001; Dunne et al., 2005). Our results indicate that dam removal, and its impacts on local ecosystem size and hydrologic connectivity and variability, may act as a disturbance that rearranges food-web compartmentalization and influences the resilience (sensu Thompson et al., 2012) of food webs. For example, the positive relationship between connectance and FCL (Figure 3.12) likely indicates that networks with more links (i.e., greater connectance) exhibit less modularity and increased trophic interactions that lengthen food chains. However, the strength of interactions and individual species traits could be more important drivers of compartmentalization and, further, longer food-chain lengths and network stability (Tylianakis et al., 2007; Thompson et al., 2012). Significant reductions in channel width at OR3 were associated with depressed fish diversity, loss of higher trophic levels, and fewer links per species and, thus, lower link density and connectance, which could have consequences for future community stability. Conversely, food-web properties at the Scioto River reaches – which only experienced minor changes in channel width – returned to pre-dam removal levels in only two years following dam removal. Thus, whereas trophic dynamics and network structure have theoretical implications for how food webs respond to disturbance, the type of disturbance and its effect on habitat and species availability will limit diversity of trophic groups, with cascading impacts on network structure and food-web stability.
Conclusions

Dams represent a major footprint of human activity and environmental change across the globe. Over 1,000 dams have been removed in the U.S. with hundreds more likely removed worldwide (O'Connor et al., 2015). The number of small-dam removal projects is expected to grow considerably in future years, making it a substantial disturbance with ecological implications for river systems across the globe. Our investigation suggests that the effects of lowhead dam removal on fish food-web dynamics is likely influenced by shifts in community structure following hydrogeomorphic changes. Additionally, the surrounding urban landscape could limit the dispersal of endemic fish species into upstream habitats or constrain the hydrogeomorphic changes necessary to promote habitat quality and availability (Wang et al., 1997). Even further, urbanization could affect the magnitude of hydrogeomorphic changes associated with dam removal (Pizzuto, 2002), and the subsequent fish-community responses. Active channel restoration played a significant role in enhancing fish diversity or network connectivity in the Olentangy River system; however, fish assemblages could take several years to respond to dam removal (Doyle et al., 2005, Kanehl et al., 1997). The shift from a lentic to lotic-type community with lower FCL and network connectivity could have implications for ecological processes, including energy transfers and future network stability. In particular, decreased connectivity could lead to lower energy transfer and resilience to secondary extinctions (Tylianakis et al., 2007).

Return to pre-dam removal food-web structure in the Scioto River suggest that larger river systems are likely less impacted by lowhead dams than their smaller
counterparts and may be more resilient to the dam-removal disturbance. As lowhead
dams continue to be removed, nuanced strategies should be considered for different size
systems, especially in urban landscapes where the restoration of fish diversity and
function is likely limited and will not promote re-colonization of rare or migratory
species dependent on high-quality habitats. Active in-stream restoration efforts should be
considered carefully, as natural recover trajectories may be equally beneficial from an
ecological standpoint. The consequences of dam removal for the ecological integrity of
river systems is dependent on a complex set of factors (e.g., land-use features, hydrologic
and sediment regimes, biotic dispersal patterns, additional restoration efforts) and, thus, a
comprehensive approach that integrates these factors will be necessary to assess the role
of dam removals in restoring freshwater systems in differing biogeographic contexts.
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Table 3.1. Definition of and metrics used to evaluate food-web properties (i.e., community-level characteristics). Modified from Romanuk et al. (2006). Properties with an * are those that were derived from the literature.

<table>
<thead>
<tr>
<th>Food web property</th>
<th>Definition of property</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species properties</strong></td>
<td></td>
</tr>
<tr>
<td>Fish species richness</td>
<td>Number of fish species in food web</td>
</tr>
<tr>
<td>Relative abundance of:</td>
<td></td>
</tr>
<tr>
<td>Top predators*</td>
<td>Proportion of species with fish prey, but no fish predators</td>
</tr>
<tr>
<td>Intermediate*</td>
<td>Proportion of species with both fish prey and predators</td>
</tr>
<tr>
<td>Basal*</td>
<td>Proportion of species with no fish prey, but fish predators</td>
</tr>
<tr>
<td><strong>Link properties</strong></td>
<td></td>
</tr>
<tr>
<td>Linkage density*</td>
<td>The number of all trophic links in the food web (L) divided by species richness (S); Links/Species ratio (L/S)</td>
</tr>
<tr>
<td>Connectance*</td>
<td>The number of all trophic links (L) divided by the maximum possible links (S^2)</td>
</tr>
<tr>
<td><strong>Chain properties</strong></td>
<td></td>
</tr>
<tr>
<td>Food chain length</td>
<td>Maximum trophic position of food web members; number of links between an apex predator and the base of the food web</td>
</tr>
<tr>
<td><strong>Web-interdependence properties</strong></td>
<td></td>
</tr>
<tr>
<td>Beta diversity</td>
<td>Turnover of species among food webs measured using the Sørensen index, an index of similarity</td>
</tr>
<tr>
<td>Homogenization*</td>
<td>Ratios of endemic to cosmopolitan species richness (Er:Cr) and abundance (Ea:Ca)</td>
</tr>
</tbody>
</table>
Table 3.2. Results from linear mixed models with fixed effects (Reach, Time, and Reach-Time interaction). * indicates a significant \((p < 0.05)\) effect.

<table>
<thead>
<tr>
<th></th>
<th>Reach</th>
<th>Time</th>
<th>Reach-Time</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(F)</td>
<td>(df)</td>
<td>(p)</td>
</tr>
<tr>
<td><strong>Olentangy River</strong></td>
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<td></td>
<td></td>
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<tr>
<td>Species Richness</td>
<td>13.21</td>
<td>3, 8</td>
<td>0.002*</td>
</tr>
<tr>
<td>T</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>I</td>
<td>8.24</td>
<td>3, 8</td>
<td>0.008*</td>
</tr>
<tr>
<td>B</td>
<td>1.17</td>
<td>3, 8</td>
<td>0.379</td>
</tr>
<tr>
<td>E±Ca</td>
<td>6.07</td>
<td>3, 8</td>
<td>0.019*</td>
</tr>
<tr>
<td>Er:Cr</td>
<td>6.35</td>
<td>3, 8</td>
<td>0.017*</td>
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<tr>
<td>Connectance</td>
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<td>Link Density</td>
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<td>FCL</td>
<td>0.88</td>
<td>3, 7,9</td>
<td>0.491</td>
</tr>
</tbody>
</table>

| **Scioto River**     |      |      |      |      |      |      |      |      |
| Species Richness     | 14.18 | 2, 6 | 0.005* | 26.5 | 2, 12 | <0.0001* | 2.2 | 4, 12 | 0.13  |
| T                    | 2.5   | 2, 6 | 0.163 | 3.33 | 2, 12 | 0.071 | 0.79 | 4, 12 | 0.556 |
| I                    | 0.05  | 2, 6 | 0.952 | 0.54 | 2, 12 | 0.594 | 4.05 | 4, 12 | 0.026* |
| B                    | 1.51  | 2, 6 | 0.294 | 3.63 | 2, 12 | 0.059 | 8.22 | 4, 12 | 0.002* |
| E±Ca                 | 6.69  | 2, 6 | 0.030* | 1.94 | 2, 12 | 0.187 | 4.2 | 4, 12 | 0.024* |
| Er:Cr                | 2.07  | 2, 6 | 0.207 | 1.45 | 2, 12 | 0.273 | 1.55 | 4, 12 | 0.249 |
| Connectance          | 0.18  | 2, 6 | 0.838 | 8.38 | 2, 12 | 0.005* | 1.85 | 4, 12 | 0.185 |
| Link Density         | 4.09  | 2, 6 | 0.076* | 42.26 | 2, 12 | <0.0001* | 5.45 | 4, 12 | 0.010* |
| FCL                  | 62.15 | 2, 5,4 | 0.0002* | 28.93 | 1, 6,4 | 0.001* | 34.21 | 2, 6,4 | 0.0004* |
**Figure 3.1.** The Olentangy and Scioto River study area in central Ohio (Columbus, OH, USA). The Olentangy River is a 5th-order, 156-km tributary of the Scioto River; the Scioto River is a 372 km, 6th-order tributary of the Ohio River. Olentangy River reaches (OR 1-4) were located upstream and downstream of the 5th Avenue Dam that was removed in August 2012. Scioto River 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 River experimental reaches, respectively. OR4 represents the downstream Olentangy River experimental reach. SR1 and SR2 represent upstream and downstream Scioto River experimental reaches, respectively. All dams (current and removed) are/were lowhead, run-of-river dams ($\leq ~7.6$ m in height). Reproduced from Dorobek *et al.* (2015).
**Figure 3.2.** Mean species richness (a – Olentangy River, b – Scioto River) and relative abundance of intermediate (c – Olentangy River, d – Scioto River) and basal (e – Olentangy River, f – Scioto River) species in control and experimental study reaches before and after dam removal. Note that before data for the Olentangy River were only available for OR1 and OR3. For the Olentangy River, black circles = OR1 (upstream control), dark gray diamonds = OR2 (passively restored), gray triangles = OR3 (actively restored), and light gray squares = OR4 (downstream). For the Scioto River, light gray squares = SR1 (upstream), gray triangles = SR2 (downstream), and black circles = SR3 (downstream control). * represents significant time effect between first and last years (Tukey’s HSD: $p < 0.05$). Dashed lines denotes significant change between two consecutive years (Tukey’s HSD: $p < 0.05$). Error bars are ± 1 SD of the mean.
Figure 3.3. Species properties for experimental and control reaches including (a) mean species richness, (b) mean relative abundance of intermediate (expressed as a proportion), and (c) basal species for Olentangy River reaches: upstream control (OR1, dark gray), upstream, passively restored (OR2, medium gray), upstream, actively restored (OR3, gray), and downstream (OR4 light gray) for each year of the study. Significant pairwise differences among reaches (per set) are indicated by different letters a, b (Tukey’s HSD: $p < 0.05$). Error bars are ± 1 SD of the mean.
Figure 3.4. Species properties for experimental and control reaches including (a) mean species richness, (b) mean relative abundance of intermediate (expressed as a proportion), and (c) basal species for Scioto River reaches SR1 (light gray), SR2 (medium gray), SR3 (dark gray) for each year of the study. Significant pairwise differences among reaches (per set) are indicated by different letters a, b, (Tukey’s HSD: $p < 0.05$). Error bars are ± 1 SD of the mean.
Figure 3.5. Mean ratio of endemic to cosmopolitan species abundance (Ea:Ca; a – Olentangy River, b – Scioto River) and richness (Er:Cr; c – Olentangy River, d – Scioto River) in control and experimental study reaches before and after dam removal. Note that before data for the Olentangy River were only available for OR1 and OR3. For the Olentangy River, black circles = OR1 (upstream control), dark gray diamonds = OR2 (passively restored), gray triangles = OR3 (actively restored), and light gray squares = OR4 (downstream). For the Scioto River, light gray squares = SR1 (upstream), gray triangles = SR2 (downstream), and black circles = SR3 (downstream control). * represents significant time effect between first and last years (Tukey’s HSD: \( p < 0.05 \)). Dashed lines denotes significant change between two consecutive years (Tukey’s HSD: \( p < 0.05 \)). Error bars are ± 1 SD of the mean.
Figure 3.6. Beta diversity as represented by the Sørensen index for between reaches and comparisons of a reach between years. Figure includes beta diversity on the Olentangy River (a) reaches where it was compared between year 1 (1), year 2 (2), and year 3 (3) and the Scioto River (b) reaches where it was compared between before (0), year 1 (1), and year 2 (2). OR1 and OR3 included a before-year 1 comparison.
Figure 3.7. Mean connectance (a – Olentangy River, b – Scioto River) and link density (c – Olentangy River, d – Scioto River) in control and experimental study reaches before and after dam removal. Note that before data for the Olentangy River were only available for OR1 and OR3. For the Olentangy River, black circles = OR1 (upstream control), dark gray diamonds = OR2 (passively restored), gray triangles = OR3 (actively restored), and light gray squares = OR4 (downstream). For the Scioto River, light gray squares = SR1 (upstream), gray triangles = SR2 (downstream), and black circles = SR3 (downstream control). * represents significant time effect between first and last years (Tukey’s HSD: $p < 0.05$). Dashed lines denote significant change between two consecutive years (Tukey’s HSD: $p < 0.05$). Error bars are ±1 SD of the mean.
![Figure 3.8](image)

**Figure 3.8.** Mean connectance (a – Olentangy River, b – Scioto River) and link density (c – Olentangy River, d – Scioto River) in control and experimental study reaches before and after dam removal. Note that before data for the Olentangy River were only available for OR1 and OR3. For the Olentangy River, dark gray = OR1 (upstream control), medium gray = OR2 (passively restored), gray = OR3 (actively restored), and light gray = OR4 (downstream). For the Scioto River, light gray = SR1 (upstream), gray = SR2 (downstream), and dark gray = SR3 (downstream control). Significant pairwise differences among reaches (per set) are indicated by different letters a, b (Tukey’s HSD: $p < 0.05$). Error bars are ± 1 SD of the mean.
Figure 3.9. Mean FCL (a – Olentangy River, b – Scioto River) in control and experimental study reaches before and after dam removal. Note that before data for the Olentangy River were only available for OR1, OR3, and SR3 for the Scioto River. For the Olentangy River, black circles = OR1 (upstream control), dark gray diamonds = OR2 (passively restored), gray triangles = OR3 (actively restored), and light gray squares = OR4 (downstream). For the Scioto River, light gray squares = SR1 (upstream), gray triangles = SR2 (downstream), and black circles = SR3 (downstream control). * represents significant time effect between first and last years (Tukey’s HSD: $p < 0.05$). Dashed lines denotes significant change between two consecutive years (Tukey’s HSD: $p < 0.05$). Error bars are ± 1 SD of the mean.
**Figure 3.10.** Mean FCL (a – Olentangy River, b – Scioto River) in control and experimental study reaches before and after dam removal. Note that before data for the Olentangy River were only available for OR1 and OR3 and SR3 for the Scioto River. For the Olentangy River, dark gray = OR1 (upstream control), medium gray = OR2 (passively restored), gray = OR3 (actively restored), and light gray = OR4 (downstream). For the Scioto River, light gray = SR1 (upstream), gray = SR2 (downstream), and dark gray = SR3 (downstream control). Significant pairwise differences among reaches (per set) are indicated by different letters a, b (Tukey’s HSD: $p < 0.05$). Error bars are ± 1 SD of the mean.
Figure 3.11. Relationships between individual fish body length (mm) and food-chain length (FCL: $R^2 = 0.221$, $p = 0.043$, $n = 19$) across all study reaches, transects, and years. Dashed lines represent confidence curves at $\alpha = 0.05$. 
Figure 3.12. Relationship between food-chain length (FCL) and connectance ($R^2 = 0.292, p < 0.0001, n = 57$) across all study reaches, transects, and years. Dashed lines represent confidence curves at $\alpha = 0.05$. 
### Supplementary Information

**Table 3.3.** Fish species collected with defined feeding guilds represented from seven study reaches on the Olentangy (4) and Scioto (3) Rivers. Basal species are those with fish predators, but not prey, intermediate species have both fish predators and prey, and top predators have no fish predators, but prey upon fish.

<table>
<thead>
<tr>
<th>Relative Trophic Position</th>
<th>Feeding Guild</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>BASAL</td>
<td>Detritivore</td>
<td>Gizzard Shad (<em>Dorosoma cepedianum</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White Sucker (<em>Catostomus commersoni</em>)</td>
</tr>
<tr>
<td>Herbivore</td>
<td></td>
<td>Bigmouth Buffalo (<em>Ictiobus cyprinellus</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Central Stoneroller (<em>Campostoma anomalum</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Northern Hogsucker (<em>Hypentelium nigricans</em>)</td>
</tr>
<tr>
<td>Omnivore</td>
<td></td>
<td>Bluntnose Minnow (<em>Pimpephales notatus</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bullhead Minnow (<em>Pimephales vigilax</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Common Carp (<em>Cyprinus carpio</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Golden Shiner (<em>Notemigonus cyrsoleucas</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Highfin Carpsucker (<em>Carpoides velifer</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quillback Carpsucker (<em>Carpoides cyprinus</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>River Carpsucker (<em>Carpoides carpio</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sand Shiner (<em>Notropis stramineus</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Smallmouth Buffalo (<em>Ictiobus bubalus</em>)</td>
</tr>
<tr>
<td></td>
<td>Insectivore (benthic)</td>
<td>Banded Darter (<em>Etheostoma zonale</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Black Buffalo (<em>Ictiobus niger</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Black Redhorse (<em>Moxostoma duquesnei</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bluebreast Darter (<em>Etheostoma camurum</em>)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fantail Darter (<em>Etheostoma flabellare</em>)</td>
</tr>
</tbody>
</table>

Continued
Table 3.3. Continued.

| Golden Redhorse (*Moxostoma erythrurum*) | Greenside Darter (*Etheostoma blenniodes*) |
| Johnny Darter (*Etheostoma nigrum*) | Logperch (*Percina caprodes*) |
| Rainbow Darter (*Etheostoma caeruleum*) | River Redhorse (*Moxostoma carinatum*) |
| Silver Redhorse (*Moxostoma anisurum*) | Slenderhead Darter (*Percina phoxocephala*) |

**Insectivore**

| Bluegill (*Lepomis macrochirus*) | Brindled Madtom (*Noturus miurus*) |
| Brook Silverside (*Labidesthes sicculus*) | Creek Chub (*Semotilus atromaculatus*) |
| Emerald Shiner (*Notropis atherinoides*) | Green Sunfish (*Lepomis cyanellus*) |
| Hybrid Sunfish (various *Lepomis* spp.) | Longear Sunfish (*Lepomis megalotis*) |
| Orange-Spotted Sunfish (*Lepomis humilis*) | Pumpkinseed (*Lepomis gibbosus*) |
| Redear Sunfish (*Lepomis microlophus*) | Silver Shiner (*Notropis photogenis*) |
| Spotfin Shiner (*Cyprinella spiloptera*) | Yellow Bullhead (*Ameiurus natalis*) |

**INTERMEDIATE**

| Black Crappie (*Pomoxis nigromaculatus*) |
| Channel Catfish (*Ictalurus punctatus*) |
| Flathead Catfish (*Pylodictis olivaris*) |

Continued
**Table 3.3. Continued**

<table>
<thead>
<tr>
<th>Fish Species</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aplodinotus grunniens</em></td>
<td>Freshwater Drum</td>
</tr>
<tr>
<td><em>Morone saxatilis x M. chrysops</em></td>
<td>Hybrid Striped Bass</td>
</tr>
<tr>
<td><em>Micropterus salmoides</em></td>
<td>Largemouth Bass</td>
</tr>
<tr>
<td><em>Ambloplites rupestris</em></td>
<td>Rock Bass</td>
</tr>
<tr>
<td><em>Micropterus dolomieu</em></td>
<td>Smallmouth Bass</td>
</tr>
<tr>
<td><em>Micropterus punctulatus</em></td>
<td>Spotted Bass</td>
</tr>
<tr>
<td><em>Morone chrysops</em></td>
<td>White Bass</td>
</tr>
<tr>
<td><em>Pomoxis annularis</em></td>
<td>White Crappie</td>
</tr>
</tbody>
</table>

**TOP PREDATORS**

<table>
<thead>
<tr>
<th>Category</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carnivore (piscivore)</td>
<td><em>Lepisosteus osseus</em> (Longnose Gar)</td>
</tr>
<tr>
<td></td>
<td><em>Esox masquinongy</em> (Muskellunge)</td>
</tr>
<tr>
<td></td>
<td><em>Stizostedion vitreum x S. canadense</em> (Saugeye)</td>
</tr>
<tr>
<td></td>
<td><em>Stizostedion vitreum</em> (Walleye)</td>
</tr>
</tbody>
</table>
Figure 3.13. Mean discharge (m$^3$ s$^{-1}$) by month on the Olentangy (a) and Scioto (b) Rivers ranging from 05/2011-10/2015. A dashed black vertical line marks removal of the (a) 5$^{\text{th}}$ Avenue dam (08/2012) and (b) Main Street dam (11/2013). Gray boxes overlay sampling months (June-October). Olentangy River discharge retrieved from USGS gauge near Worthington, Ohio (40°06’37’’, 83°01’55’’). Scioto River discharge retrieved from USGS gauge south of downtown Columbus, Ohio (39°54’34’’, 83°00’33’’).
Figure 3.13. Linear regression of number of links to species richness ($R^2 = 0.952, p < 0.0001, n = 69$) across all study reaches, transects, and years. Dashed lines represent confidence curves at $\alpha = 0.05$. 
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Appendix A. Ohio Division of Wildlife collection permits

Division of Wildlife Headquarters
2045 Morse Road, Bldg. G
Columbus, Ohio 43229-6693
1-800-WILDLIFE

WILD ANIMAL PERMIT: 15-49

SCIENTIFIC COLLECTION

MAZEKA SP SULLIVAN
OHIO STATE UNIVERSITY
SCHOOL OF ENVIRONMENTAL & NAT. RES., 210 KOTTMAN
COLUMBUS, OH 43210

SPECIAL SECURITY NUMBER: XXX-XX-2071

Scott Zody
Chief, Division of Wildlife

DATE ISSUED
3/29/2012

Others authorized on permit
(SEE ATTACHMENT)

Revised: 6/25/2013

is hereby granted permission to take, possess, and transport at any time and in any manner specimens of wild animals, subject to the conditions and restrictions listed below or any documents accompanying this permit.

This permit, unless revoked earlier by the Chief, Division of Wildlife, is effective from:
3/16/2012 to:
3/15/2015

This permit must be carried while collecting wild animals and be exhibited to any person on demand.

THIS PERMIT IS RESTRICTED TO THE FOLLOWING:

1. Permittee must notify the Division of Wildlife of each study site location for mussel surveys and receive prior approval before conducting collection activities. Contact John Navarro at john.navarro@dnr.state.oh.us.
2. Permittee may collect fish, birds, reptiles, amphibians, mussels and macroinvertebrates for survey and inventory. Raccoons may also be live trapped for research. No sport fish over six inches may be retained. Mussels may not be removed from the site and must be immediately released to the collection location upon identification.
3. Areas where the northern ruffle shell and clubshell have been reintroduced must be avoided.
4. Permittee may collect blood and feather samples from birds. A USFWS permit is required for migratory species.
5. Any specimen held longer than 30-days must be humanely euthanized or retained for further research/education.
6. Contact the Division if undocumented aquatic invasive species are discovered.
7. Twenty-four hours prior to collecting activities, permittee must contact the local wildlife officer or nearest wildlife district office to advise locations and duration of sampling.
8. All traps must be clearly labeled with the contact information of the responsible person. Traps must be checked each calendar day.
9. All voucher specimens are to be deposited at The OSU, Museum of Biological Diversity or the Cleveland Museum of Natural History.
10. Collection is prohibited in the Killbuck, tributaries to and east branch of the Chagrin River above I-90, Fish Creek (Williams County) and Division of Wildlife property without explicit written permission from the Division of Wildlife.

Sampling is further restricted in streams that may have federally listed mussels. See the enclosed "USFWS Restricted Streams of Ohio" document for a list of streams and contact information.

***Permission is granted for mussel work in the Darby Watershed. Electroshocking only is permitted in the Big Darby.

Locations of Collecting
STATEWIDE WITH NOTED EXCEPTIONS

Equipment and method used in collection:
ELECTROSHOCKER, SEINES, BLOCK NETS, DIP NETS, HOOP NETS, MINNOW TRAPS, SURBER SAMPLES, MIST NETS, HAND NETS, BOX TRAPS AND ROCKET NETS

Name and number of each species to be collected:
FISH, BIRDS, MACROINVERTEBRATES, MUSSELS, REPTILES, AND AMPHIBIANS. RACCOONS MAY BE LIVE TRAPPED FOR OBTAINING TISSUE SAMPLES. SAMPLING BY ELECTROSHOCKING ONLY ARE PERMITTED IN THE BIG DARBY.

RESTRICTIVE DOCUMENTS ACCOMPANYING THIS PERMIT? YES

NO ENDANGERED SPECIES MAY BE TAKEN WITHOUT WRITTEN PERMISSION FROM THE CHIEF
ATTACHMENT

This attachment to Scientific Collecting Permit # 15-46 authorizes the following persons to conduct the activities listed on the permit, within the conditions and restrictions set forth. Each person must carry and exhibit upon request, a copy of the permit and this attachment when conducting any of the listed activities. The person named on the permit assumes full responsibility for the actions of the persons on this list and for completing and submitting all required reports.

<table>
<thead>
<tr>
<th>Name</th>
<th>SSN or Driver License</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADAM KAUTZA</td>
<td>XXX-XX-7593</td>
</tr>
<tr>
<td>LARS MEYER</td>
<td>XXX-XX-6382</td>
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<tr>
<td>LESLIE RIECK</td>
<td>XXX-XX-5995</td>
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<td>DANIELLE VENT</td>
<td>XXX-XX-0894</td>
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<td>ALAYNA DOROBEK</td>
<td>XXX-XX-8706</td>
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<td>KRISTEN SHEARER</td>
<td>XXX-XX-9595</td>
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WILD ANIMAL PERMIT: 18-91

DATE ISSUED: 4/24/2015 Revised: 10/8/2015

MAZEKA SP SULLIVAN
OHIO STATE UNIVERSITY
SCHOOL OF ENV. & NAT. RES., 210 KOTTMAN HALL, 202
COFFEY RD.
COLUMBUS, OH 43210

is hereby granted permission to take, possess, and transport at any time and in any manner specimens of wild animals, subject to the conditions and restrictions listed below or any documents accompanying this permit. This permit, unless revoked earlier by the Chief, Division of Wildlife, is effective from:

4/24/2015 to: 3/15/2018

The Chief of the Division of Wildlife will not issue permits for Dangerous Wild Animal (DWA) species (ORC 935.01 except native DWA, required for specific projects. The permit issued by the Chief does not relieve the permittee of any responsibility to obtain a permit pursuant to R.C. Chapter 935 except as specified for the animals and purposes permitted herein. The permittee must adhere to all additional requirements under R.C. Chapter 935.

THIS PERMIT IS RESTRICTED AS FOLLOWS:

1. Permittee must notify the Division of Wildlife of each study site location for mussel surveys and receive prior approval before conducting collection activities. Contact John Navarro at john.navarro@dnr.state.oh.us.
2. Permittee may collect fish, birds, reptiles, amphibians, mussels and macroinvertebrates for survey and inventory. Raccoons may also be live trapped for research. No sport fish over six inches may be retained. Live mussels may not be removed from the site and must be immediately released to the collection location upon identification. Dead shells only may be removed and added to the mussel reference collection held at Schermeyer Olentangy River Wetland Research Park.
3. Areas where the northern riffleshell and clusheash have been reintroduced must be avoided.
4. Permittee may collect blood and feather samples from birds. A USFWS permit is required for migratory species.
5. Any specimen held longer than 30-days must be humanely euthanized or retained for further research and education.
6. Please notify John Navarro by email or phone at 614-365-6715 if a new location for a state-listed species is found. Contact Mr. Navarro within 24 hrs if an undocumented invasive species is found.
7. Twenty-four hours prior to collecting activities, permittee must contact the local wildlife officer to advise locations and duration of sampling.
8. All traps must be clearly labeled with the contact information of the responsible person. Traps must be checked each calendar day.
9. All voucher specimens are to be deposited at The CSci, Museum of Biological Diversity Schermeyer Olentangy River Wetland Research Park or the CMNH.
10. Collection is prohibited in the Killbuck, tributaries to and east branch of the Chagrin River above I-90, Fish Creek (Williams County) and Division of Wildlife property without explicit written permission from the Division of Wildlife. Sampling is further restricted in streams that may have federally listed mussels. See Appendix A of the Ohio Mussel Survey Protocol (April 2014 @ http://wildlife.ohiodnr.gov/licenses-and-permits/specialty-licenses-permits) for locations of federally listed mussels.
**Permission is granted for mussel work in the Darby Watershed. Electroshocking only is permitted in the Big Darby.
11. Permittee must provide an annual electronic report of collecting activities in the Diversity Database Excel spreadsheet to the Division of Wildlife. A copy of any published materials that result from this project should also be forwarded to the division.

Locations of Collecting:

STATEWIDE WITH NOTED EXCEPTIONS

Equipment and method used in collection:

ELECTROSHOCKER, SEINES, BLOCK NETS, DIP NETS, HOOP NETS, MINNOW TRAPS, SURBER SAMPLES, MIST NETS, HAND NETS, BOX TRAPS AND ROCKET NETS

Name and number of each species to be collected:

FISH, BIRDS, MACROINVERTEBRATES, MUSSELS, REPTILES, AND AMPHIBIANS. RACCOONS MAY BE LIVE TRAPPED FOR OBTAINING TISSUE SAMPLES. SAMPLING BY ELECTROSHOCKING ONLY ARE PERMITTED IN THE BIG DARBY.

RESTRICTIVE DOCUMENTS ACCOMPANYING THIS PERMIT? YES

NO ENDANGERED SPECIES OR AQUATIC NUISANCE SPECIES MAY BE TAKEN WITHOUT WRITTEN PERMISSION FROM THE CHIEF.
ATTACHMENT

This attachment to permit # 18-91 authorizes the following persons to conduct the activities listed on the permit, within the conditions and restrictions set forth. Each person must carry and exhibit upon request, a copy of the permit and this attachment when conducting any of the listed activities. The person named on the permit assumes full responsibility for the actions of the persons on this list and for completing and submitting all required reports.

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Appendix C. Stable-Isotope Data for all Fish and Basal Resources from the Olentangy and Scioto River reaches from Chapter 3

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The preceding common and scientific names are updated based on American Fisheries Society Special Publication 29, Common and Scientific Names of Fishes from the United States, Canada, and Mexico, Sixth Edition, 2004.

Feeding Guild Codes: P-Piscivore; F-Filter Feeder; I-Insectivore; O-Omnivore; V-Invertivore; Generalized Insectivore; H - Herbivore; C - Carnivore (Fish, Large Invertebrate).
Tolerance Codes: I - Intolerant (also (R,S), M - Moderately Intolerant; No Code - Intermediate Tolerance; P - Moderately Tolerant; T - Tolerant. ["Sensitive" species are Intolerants and Moderately Intolerant].
IBI Group: E - Exotic; F - Sport Fish; R - Round Bodied Sucker; C - Deep Bodied Sucker; W - White Sucker; N - Minnow; S - Sunfish; D - Darter; G - Carp/Goldfish.
Breeding Guild: N - Complex, No Parental Care; S - Simple Lithophil; M - Simple, Misc; C - Complex, Parental Care.

11/08/2006