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PRIMARY RESEARCH PAPER

Dispersal limitations on fish community recovery following long-term water quality remediation

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Abstract In-stream barriers may impose constraints on the ecological effectiveness of restoration strategies by limiting colonization. We assessed the importance of dispersal limitations to fish community recovery following long-term pollution abatement, water quality remediation, and species introductions within the White Oak Creek watershed near Oak Ridge, Tennessee (USA). Long-term (26 years) responses in fish species richness, biomass, and community composition to water quality remediation were evaluated in light of physical barriers (culverts and weirs). We found that barriers to dispersal were potentially limiting fish community recovery by preventing colonization by introduced species and seasonal migrants. Changes in richness were negatively related to barrier index, a measure of the degree of isolation by barriers. Following introductions, upstream passage for six fish species above non-passable barriers was not observed. Highly isolated sites were dominated by a few equilibrium species, whereas less isolated sites showed more variation in life history strategies with increasing periodic and opportunistic strategists. The importance of barriers on community dynamics decreased over time—an indication of increasing community stability, homogenization of fauna, and improved water quality. However, isolating the role of dispersal limitation was complicated by multiple interacting stressors, such as the compounding effects of barriers and pervasive water quality conditions.

Keywords Stream fragmentation · Restoration ecology · Culvert · Fish passage · Habitat patches · Connectivity

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Introduction

The ability of organisms to disperse among habitat patches is essential for sustaining viable populations and diverse communities (Brudvig et al., 2010; Keller et al., 2012; Perkin & Gido, 2012). A growing body of literature exists documenting the deleterious effects of habitat fragmentation on both terrestrial (Herkert, 1994; Brudvig et al., 2010) and aquatic organisms (Newton et al., 2008; Perkin & Gido, 2012), as well as the importance of preserving and restoring migration corridors to adequately protect species from decline or extirpation (Dixon et al., 2006; Kiffney et al., 2009).

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Although habitat fragmentation is presumed to be the most impactful to highly migratory species (e.g., diadromous fish) (Meixler et al., 2009), recent studies suggest that habitat fragmentation is also extremely important to organisms with seemingly small home ranges (Skalski et al., 2008) or sessile organisms (e.g., mussels, plants) that rely on mechanisms other than migration for dispersal of offspring (Newton et al., 2008; Brederveld et al., 2011). This is especially true for small stream communities that primarily comprised small fish species. Small fish species have been shown to move extensive distances (scale of 10^1 km) to colonize new areas following local extinctions or preserve gene flow (Albanese et al., 2009; Hitt & Angermeier, 2011). Not surprisingly, barriers to in-stream movement have been shown to influence small-fish spatial distribution (Han et al., 2008), population dynamics (Warren & Pardew, 1998; Favaro et al., 2014), and genetic structure (Skalski et al., 2008).

Connectivity among habitats is important to the effectiveness of habitat enhancement aimed at supporting species conservation efforts. Unfortunately, many habitat enhancement projects are implemented without considering whether the true limitation of populations is, in fact, habitat condition as opposed to habitat connectivity (Schrott et al., 2005; Miller & Hobbs, 2007). Without ensuring that the potential exists for recolonization following habitat enhancement, many conservation efforts have been ineffective (Lepori et al., 2005) or, even worse, harmful to populations (McManamay et al., 2013). Unlike habitat enhancements (e.g., boulder placement), water quality remediation is a process-driven restoration approach, which requires larger-scale, holistic management strategies (Roni et al., 2008). For example, projects with the goal of improving water quality include implementing best management practices for agriculture, revegetating floodplains, creating wetlands, creating riparian buffers, or stormwater management, all of which are conducted at scales larger than the immediate stream reach (Sudduth et al., 2007).

Improvements in water quality have proven effective in the recovery of macroinvertebrate (Bednarek & Hart, 2005; Smith et al., 2011) and fish communities (Ryon, 2011; Southworth et al., 2011). Within a four-state region of the Southeastern US, water quality restoration is at least a $500 million enterprise, making up 33% of total restoration projects and 45% of total restoration project costs (Sudduth et al., 2007). In comparison, dam removals and fish passage enhancements are 10 times less common than water quality improvements within the same region (Sudduth et al., 2007). Given the importance of habitat connectivity in restoration projects, it becomes of practical importance to understand the limitations of colonization potential on water quality improvement projects. Furthermore, empirical assessments of dispersal limitations on restoration effectiveness are rare (Brederveld et al., 2011; Kubach et al., 2011), especially in cases where process-driven restoration is implemented at scales greater than immediate stream reaches and is focused on remediating chronic perturbations, like poor water quality conditions. Lastly, barriers are likely to compound the effects of poor habitat conditions (Perkin et al., 2015); thus, multidimensional views are needed to restore stream ecosystems impacted from a complex mixture of disturbances.

Herein, we address the importance of dispersal limitations to fish community recovery following long-term water quality remediation across the White Oak Creek (WOC) watershed near Oak Ridge, Tennessee (USA). Under the Environmental Response, Compensation, and Liability Act of 1980, the U.S. Department of Energy (DOE) initiated water quality remediation campaigns at their facilities across the U.S., including Oak Ridge National Laboratory (ORNL) (Peterson, 2011). Construction and operations of facilities at ORNL have contributed to significant impacts, including stream channelization, sedimentation, and increased contaminant loads to surface water and groundwater within WOC. Since the late 1980s, several pollution abatement and remediation projects have been completed such as remediating soils and groundwater contamination, controlling point-source discharges, and species introductions (UCOR, 2011). However, the recovery of fish communities in WOC has been limited and dependent upon species introductions. Due to highly fragmented habitats in WOC, we hypothesized that habitat fragmentation may be playing a role in limiting recovery of the fish community in WOC watershed.

Materials and methods

Study site description

The WOC watershed is approximately 16.8 km^2 and is entirely located within the U.S. Department of Energy

Oak Ridge Reservation (ORR) in southeastern Tennessee, USA (Fig. 1). The stream flows through the ORNL campus and then joins Melton Branch, which creates a 4th order stream that discharges into the Clinch River 3.7 km downstream of Melton Hill dam. The lower portion of the stream is impounded creating White Oak Lake (7 ha), a shallow reservoir embayment experiencing high siltation and sedimentation. Elevation ranges from 226 m at the mouth of the Clinch River to 413 m in the Melton Branch portion of the watershed. Most of the headwaters and the lower stream section have intact riparian zones with gravel and cobble substrates, but may experience dry channels during low-flow months. The portion flowing through the ORNL campus is impacted by historical channelization and little riparian cover. This reach is also augmented by treated and untreated effluents and water discharges from several cooling towers which, at times, influence the temperature and chemistry of the stream (Sherwood & Loar, 1987).

Background

During the 1940–1950s, wastewater discharges from ORNL facilities had considerable contaminant loads including heavy metals, polychlorinated biphenyls (PCBs), and mercury, which are still present in legacy sediments and outfalls from buildings. Until 1996, many discharges from once-through cooling facilities contained high amounts of chlorinated water. Beginning with the issuance of a National Pollutant Discharge Elimination System Permit, water quality remediation actions were implemented across the ORR, including ORNL (Southworth et al., 2011). Since 1985, remediation activities have been widespread in WOC and have included improvements to water treatment facilities, dechlorination of effluents, modifications to cooling towers, proper waste burial, and riparian restoration (Fig. 2). Despite intensive remediation programs, the fish community response to water quality improvements in WOC did not reflect other ORR streams receiving remedial activities from similar or even more intense impacts (e.g., Ryon, 2011). For example, resident communities lacked several major taxonomic groupings of fish which were once common in WOC (Krumholz, 1954) and are found in adjacent watersheds (Ryon, 2011). To compensate for the lack of biological recovery, a fish introduction program was initiated in 2007. Based on regional expertise of local fish fauna (Ryon & Loar, 1988; Etnier & Starnes, 1993), six fish species were selected for introduction into WOC: striped shiner (*Luxilus chrysocephalus*), bluntnose minnow (*Pimephales notatus*), northern hogsucker (*Hypentelium nigricans*), rock bass (*Ambloplites rupestris*), snubnose darter (*Etheostoma simoterum*), and stripetail darter (*Etheostoma kennicotti*). These fish were introduced at six locations within the watershed based on species-specific habitat needs (Supplementary Material 1).

Fish community monitoring

Fish community sampling and population analysis follows Ryon (2011). Fish communities were sampled at 11 sites in WOC during both the spring (Mar–May) and fall (Sept–Oct) from 1985 through 2013. Sites (50–100 m reaches, depending on stream size) were located on 1st–4th order streams (1–7 m wetted width) and were sampled with one or two backpack electrofishing units using block nets at the up- and downstream ends. All collected fish were identified, weighed, and measured for length. Surface area of each reach was measured using wetted widths taken at 5-m intervals following sampling. Based on maximum-likelihood methods (Carle & Strub, 1978), a comprehensive Fortran 77 program was used to estimate population density and biomass density (Railsback et al., 1989).

Quantifying fragmentation and additional stressors

Characterizing barriers

Locations of road crossings and in-stream structures (i.e., weirs and flumes) were identified using maps, aerial imagery, and discussions with water quality experts on the ORNL reservation. At each location, GPS coordinates, photographs, and measurements of physical characteristics of each structure were recorded. In cases where structures had multiple components (i.e., side-by-side culverts), measurements were made separately for each individual component. The type, material, dimensions, gradient, water velocity, and outlet drop of each structure were recorded. Substrate conditions within each structure and the depth of the plunge pool below each structure were also recorded. For a summary of physical

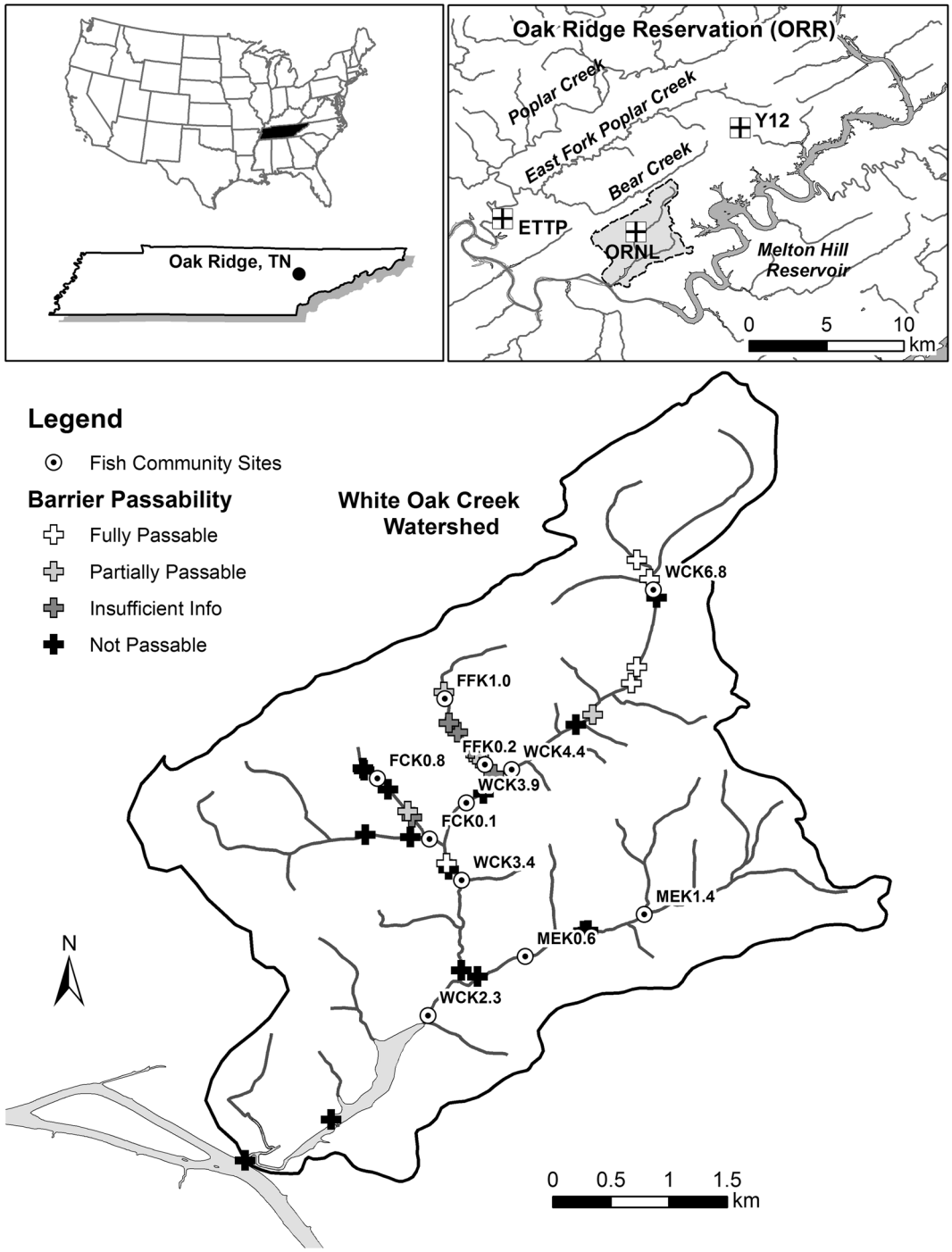


Fig. 1 Fish community sites and barriers within the White Oak Creek watershed, near Oak Ridge, Tennessee. *Upper right panel* shows the Oak Ridge Reservation, including the locations of Oak Ridge National Laboratory (ORNL), Y12-National Security Complex, and East Tennessee Technology Park (ETTP) in relation to White Oak Creek (WOC) watershed. Barriers within WOC are labeled according to passage potential. See Table 1 for details of fish community sites

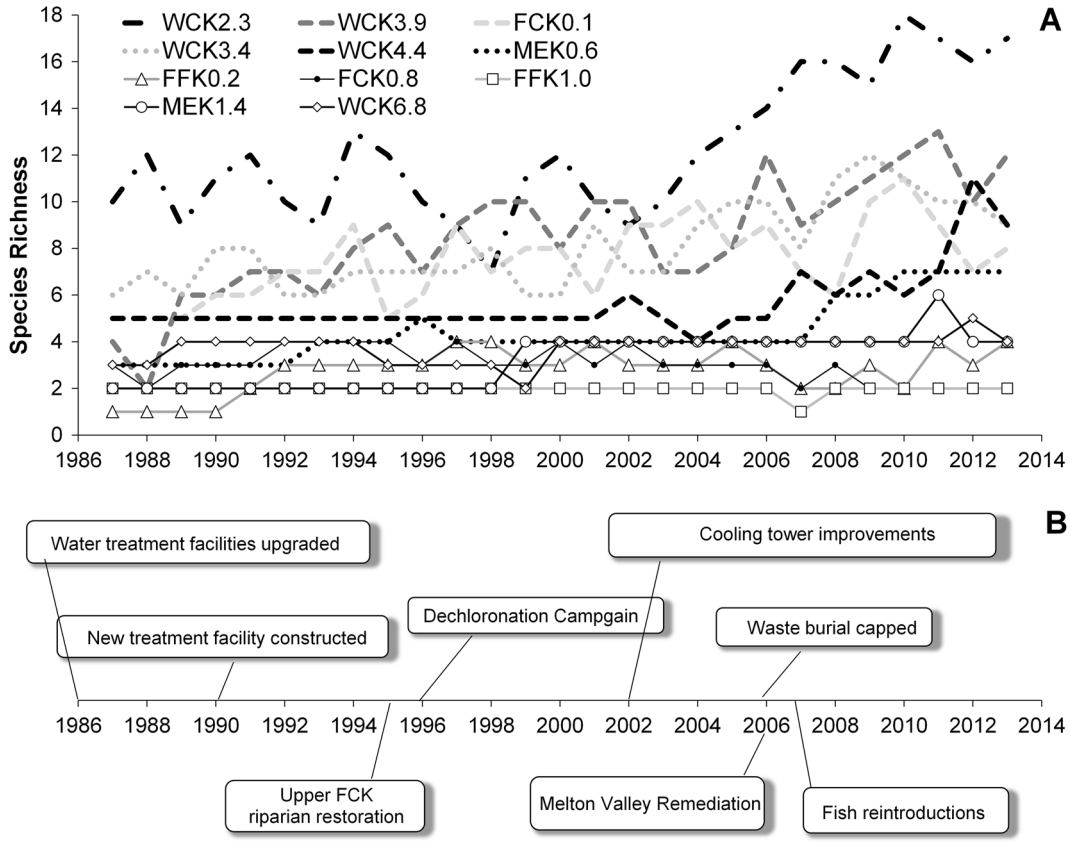


Fig. 2 **A** Total species richness (combined spring and fall) for each site and year. *Bold dashed lines* represent sites with clear increases in richness, whereas lighter *solid lines* with *symbols* represent sites with less-noticeable increases in richness. **B** Chronology of major examples of pollution abatement and water quality remediation actions within the White Oak Creek watershed (list is not exhaustive). Note that the dates mark the initiation (pollution abatement) or completion (remediation actions) of different programs, which have cumulative effects on water quality improvement over time

measurements and methodology needed for assessing fish passage, see Mahlum et al. (2014a).

Based on the types of potential barriers found in WOC watershed, U.S. Forest Service's FishXing2 software (www.stream.fs.fed.us/fishxing/Version2.html) was used to evaluate the passage potential of structures for five species, representing a wide range of fish body morphologies: striped shiner, bluntnose minnow, northern hogsucker, snubnose darter, and banded sculpin (*Cottus carolinae*). Swimming and leaping abilities were obtained using a combination of laboratory studies and literature review for each species. Five individuals of each species were collected in streams near WOC watershed and were returned to the laboratory where they were held in tanks for 2–3 days to acclimate. Each individual was then placed in a circular flume where flow was incrementally increased at 5 cm/s at 5-min intervals (maximum attainable velocity = 1 m/s). Maximum prolonged swim speed was recorded when individuals stopped swimming, failed to hold the position in the current, or were impinged on the screen at the back of the chamber. Average (± SD) values for maximum prolonged swim speeds (cm/s) of each species were 27.0 (11.3), 29.8 (6.0), 33.6 (2.4), 37.5 (9.6), and 50.8 (2.8) for banded sculpin, bluntnose minnow, snubnose darter, northern hogsucker, and striped shiner, respectively. Burst speeds and leaping ability (height) for similar species were obtained from literature review (e.g., Meixler et al., 2009; Ficke et al., 2011). These results along with physical characteristics of each barrier were then included as input in the FishXing2 software to obtain the estimates of passage potential (see Mahlum et al. (2014a) for details). One limitation of this analysis is

Table 1 Site summary characteristics for cumulative length (Cum_L), fragmentation indices, and significant outfalls

Site	Cum length (km)	Fragment length (km)			Dendritic connectivity index			Barrier index			Outfall flux ratio	
		All	PP	NP	All	PP	NP	All	PP	NP	500 m	Frag
FCK0.8	0.34	0.24	0.24	0.24	0.05	0.05	0.05	−0.01	−0.02	0.05	0.00	0.00
FFK1.0	0.75	0.29	0.29	1.72	0.05	0.05	0.27	0.86	0.92	−0.09	0.00	0.00
FFK0.2	1.42	0.24	0.24	1.73	0.04	0.04	0.27	0.01	0.02	−0.04	0.13	0.05
WCK6.8	3.60	0.96	3.69	3.69	0.09	0.35	0.35	0.18	0.40	−0.41	0.00	0.00
FCK0.1	4.30	0.58	0.63	0.91	0.07	0.07	0.11	−0.18	−0.17	−0.03	0.03	0.00
MEK1.4	5.70	6.15	6.15	6.15	0.61	0.61	0.61	−0.28	−0.35	0.35	0.08	0.08
MEK0.6	7.91	1.73	1.73	1.73	0.15	0.15	0.15	−0.09	−0.21	0.24	0.00	0.00
WCK4.4	8.35	2.05	2.05	2.05	0.15	0.15	0.15	−0.04	−0.02	−0.02	0.10	0.24
WCK3.9	10.3	0.72	0.78	0.78	0.05	0.05	0.05	−0.09	−0.11	−0.08	0.19	0.21
WCK3.4	16.1	0.97	0.97	0.97	0.05	0.05	0.05	−0.16	−0.24	0.01	0.04	0.00
WCK2.3	26.7	1.93	2.99	2.99	0.07	0.10	0.10	−0.11	−0.12	−0.02	0.00	0.00

that we consider permeability of structures temporally static, as physical measurements were made during summer conditions. However, it should be noted that passage potential may increase during higher flow conditions. Because FishXing tends to produce conservative assessments of passage potential (Mahlum et al., 2014a), calculating species-specific passage potential of each structure would be uncertain; thus, we created two highly divergent fish passage groups [(1) only striped shiners and (2) all other species], and four structure groups [(1) fully passable to all species, (2) partially passable to only shiners, (3) not passable, or (4) insufficient in determining passage potential]. Structures with insufficient information were typically box culverts extending >60 m long and with no way to determine gradient and streambed material, or whether additional potential barriers were present within the structure. For all subsequent analyses, we combined these structures with partially passable structures.

Fragmentation indices

The most intuitive measure of stream fragmentation is fragment length, i.e., connected distance between up- and downstream barriers (Worthington et al., 2014). However, this does not provide a measure of the likelihood of movements among stream patches. Cote et al. (2009) developed a Dendritic Connectivity Index (DCI), which provides a measure of coincidence probability related to fragmentation, i.e., the probability that a fish can move between fragments. DCI is flexible as calculations can be catered to diadromous fish or potadromous fish species. Fragment length and DCI, while easily calculated, do not provide a measure of population isolation due to barriers. Because distances among populations also induce isolation, spatial autocorrelation should be accounted when considering isolation by barriers.

Using the high-resolution National Hydrography Dataset (1:24 k) (nhd.usgs.gov), we calculated three different measures of fragmentation for each fish community monitoring site: (1) fragment length (km), (2) DCI, and (3) a barrier index. Each measure was calculated under three scenarios: (1) all barriers regardless of passage potential (all); (2) only barriers that were partially passable, had insufficient information, or were non-passable (pp), and (3) only non-passable barriers (np). For each fish community site, fragment length (FL) was measured as the total stream distance (in km), including tributaries, bounded on the up- and downstream ends by barriers. This resulted in three measures where $FL_{\mathrm{all}} \leq FL_{\mathrm{pp}} \leq FL_{\mathrm{np}}$. Because DCI is a measure of connectivity for an entire stream network, we only considered DCI for the immediate stream segment to consider each fish community site separately using the following equation:

$$\mathrm{DCI} = \frac{l_1}{L_{\mathrm{up}}}, \tag{1}$$

where l_1 is the fragment length of the immediate stream segment containing the fish community site and L_{up} is the cumulative length of stream segments upstream. Using L_{up} as the denominator, Eq. 1 provides a coincidence probability of the segment

length given its relative position in the watershed (as to provide a scaling factor). Similar to FL, DCI was measured for the all, pp, and np scenarios.

Lastly, we introduce a barrier index (BI) as a measure of barrier-induced isolation among populations that controls for spatial autocorrelation while assessing the frequency of barriers among populations, i.e., fish community sites. In a fragmented watershed, the number of barriers is expected to increase with distance between each population and thus

$$[B]_{ij} \sim f([X]_{ij}), \tag{2}$$

where B and X represent matrices of the number of barriers and distances, respectively, between pairwise combinations among each ith and jth population. BI is calculated for each population as

$$BI_i = \frac{\sum_{ij}^{n} (B_{ij} - \bar{B}_{ij})}{n}, \tag{3}$$

where B and $\bar{B}$ are the observed and expected numbers of barriers, respectively, between the ith and jth population and n is the total number of pairwise comparisons between a given population and all other populations. In WOC, there are 11 fish community sites and thus $n = 10$. A partial Mantel correlogram was developed in the R programming environment using the pmgram function (ecodist package) to relate the number of barriers to pairwise river distances among populations (Goslee & Urban, 2015). Predicted numbers of barriers were obtained and compared to the observed number of barriers to calculate BI for each fish community site.

Additional stressors and watershed characteristics

Episodic effluent discharges from outfalls in WOC have been directly linked with fish kills and may further limit ecological recovery in the WOC. The location and discharge capacity (L s^{-1}) of outfalls, representing significant point-source discharges of chlorinated water and warm water from facilities and cooling towers, were used to assess the potential effects of episodic poor water quality conditions on fish communities. The cumulative outfall discharge capacity was summarized for outfalls occurring within 500 m upstream (Out_500 m) and within each fragmented segment (Out_frag). Multiple stream gages in the WOC were used to develop drainage area–discharge relationships and estimate stream flow discharge at each site. Out_500 m and Out_frag were divided by the estimated stream flow discharge at each site to calculate outfall flux as a dimensionless ratio.

Other factors likely to influence fish community included the spatial location of each site within the watershed and the proximity of each site to other community sites. As an assessment of stream size, we measured the cumulative length of stream upstream of each site (CumL). Because distance among community sites may be an indication of population isolation, we used the river distance matrix to create Eigenvectors that represent the spatial autocorrelation among fish community sites. We used the Principal Coordinates of Neighborhood Matrix (pcmn) function in *R* (vegan package) to transform the distance matrix into distance vectors without a specified truncation threshold (all sites are neighbors) (Borcard & Legendre, 2002; Oksanen et al., 2011). Eigenvectors explaining significant amounts of variation in the spatial arrangement of sites were determined using the broken-stick method (Jackson, 1993).

Ecological recovery and fragmentation

In order to determine the effects of fragmentation on fish community recovery, four approaches were used: (1) species' range expansion in relation to barriers, (2) relating temporal changes in fish richness/biomass to fragmentation, and (3) evaluating trends in fish community and fish trait composition in relation to fragmentation. All trends were examined in light of species introductions (pre- and post-2007).

Species distributions

Following introductions, distributions of species' presences and absences reflect the impact of barriers on dispersal but also distance from release sites. Because species introduced into WOC were previously absent, tagging individuals was unnecessary for examining distributions. Based on release sites, survey locations, and impassable barriers, we divided WOC into several reaches (Supplementary Material 1). Presence/absence of fish species in each reach was determined via routine community monitoring surveys

(3-pass depletion) twice per year at each site, but augmented with single-pass qualitative surveys that covered longer stretches up- and downstream from each site (500-m reaches) once a year. We determined population establishment if either young-of-the-year were observed or adults were observed in increasing numbers more than one year.

Trends in richness and biomass

Based on 26 years of bi-annual fish community monitoring (1987–2013), models were developed to quantify the effects of sites on changes in richness and biomass before and after species introductions were initiated (2007). A generalized linear mixed model (GLMM) was used to model richness as a Poisson distribution, whereas biomass was $\log(x + 1)$ transformed and modeled using a linear mixed model. Because the sampling design constituted repeated measures, site was nested within season as a random effect. Site, year, and site*year interactions were modeled as fixed effects. Models were constructed using the glmer and lmer functions in the lme4 package in R (Bates et al., 2015). Separate models were used for years prior to 2007 and for all years to determine effects of species introductions. Site*year coefficients were compared to fragmentation indices, water quality stressors, and watershed characteristics using Spearman's rank correlations.

Temporal dynamics in fish community and trait composition

Temporal trends in the importance of environmental variables in organizing community composition were examined using Non-metric Multidimensional Scaling (NMDS). Fish community sites were examined in ordination space using Bray–Curtis dissimilarities in relative species population densities for both seasons within each year, together and individually. Relative densities were arcsine-square-root-transformed prior to ordination. NMDS was conducted using the metaMDS function (vegan package) in R using 100 different initial configurations and 200 iterations. Stress values were examined to ensure that final solutions were stable. For each ordination, fragmentation indices, outfall flux, and watershed characteristics were tested for correlation with NMDS axes using the envfit function (vegan package), which adjusts the projection of ordination points to have maximum correlation with environmental vectors. The envfit function provides a squared correlation coefficient, R^2, as a measure of vector importance for each environmental variable. We examined temporal trends in vector importance for the entire period. We hypothesized that streamflow conditions may influence the year-to-year importance of fragmentation and water quality on fish assemblage composition, where low flows exacerbate conditions and higher flows alleviate barrier limitations. Daily streamflow records were obtained from USGS gauge 03536550 near the center of the watershed. Records were collected by USGS from 1985 until 2001, after which monitoring was continued by ORNL. Descriptive statistics (average, minimum, maximum, and CV) were calculated for different temporal periods: annual, winter (Dec–Mar), and summer/fall (June–Oct) to reflect flow conditions prior to sampling events. We examined relationships between vector importance and flow metrics using Spearman's rank correlations, under no time lags, 1-year time lags, and 2-year time lags.

In order to generalize changes in the composition of the fish community, we employed a trait-based approach, which consolidates information across taxonomic groups into shared adaptive strategies. Specifically, fish life history strategies are well suited for examining community recovery to disturbance as they represent major tradeoffs among juvenile survival, parental care, fecundity, body size, and longevity (Winemiller & Rose, 1992). These tradeoffs are represented by a continuum within three endpoints. Periodic species are large-bodied fish characterized by late maturation, high fecundity, and low parental investment. Equilibrium species are smaller-bodied fishes with lower fecundity but higher parental care and higher juvenile survival. Opportunistic fishes are small-bodied fish with early maturation, no parental investment, and extended spawning seasons with multiple bouts. Because periodic species prefer predictable conditions to support migrations (Winemiller, 2005), we hypothesized that periodic species would be prevalent in less isolated sites or sites with longer fragment lengths. In contrast, equilibrium species display density-dependent population organization and prefer stabile, resource-limited environments; thus, we predicted that communities at highly isolated sites would be dominated by equilibrium strategists. However, reaches that experience episodic disturbances might favor opportunists.

Because life history strategies are more accurately viewed as a continuum within the tri-point space, assessing life history strategy on the basis of distance from each endpoint may be preferred over hard assignment. The affinity of a fish species for a given life history strategy was based on minimum Euclidean distance from each species multivariate position and each life history group's endpoint (Mims et al., 2010, McManamay and Frimpong, 2015). Multivariate distances from each endpoint were based on maximum length, age at maturation, longevity, fecundity, parental care, and the ability to have multiple spawning bouts (see McManamay and Frimpong (2015) for more details). For each species, we scaled Euclidean distances from 0 to 1 and then calculated inverse values (e.g., higher value for equilibrium suggests more affinity for that strategy). These inverse values were then multiplied by the densities of each species, and used to calculate relative life history densities for each site. On the basis of barrier index values, we then partitioned sites into "highly isolated" (*BI*_all >0) and "less isolated" (*BI*_all <0) groups. Temporal patterns in life history composition at highly isolated and less isolated sites were examined using ternary plots (robCompositions package in R programming environment) (Templ et al., 2015).

Results

Fish communities

A total of 27 fish species (22 native to the basin) were detected within the WOC watershed across 26 years of sampling. Western blacknose dace (*Rhinichthys obtusus*), largescale stoneroller (*Campostoma oligolepis*), creek chub (*Semotilus atromaculatus*), and banded sculpin were detected at the majority of sites (Appendix 1). Sunfish were also common with redbreast sunfish (*Lepomis auritus*), largemouth bass (*Micropterus salmoides*), and bluegill (*Lepomis macrochirus*) being the most widespread. Five of the six introduced species became established within the watershed and viable populations were more common at sites further downstream in the watershed (Appendix 1). The furthest downstream site (WCK2.3) was influenced by occasional migrants residing in White Oak Creek Lake, such as golden redhorse (*Moxostoma erythrurum*), spotted sucker (*Minytrema melanops*), and gizzard shad (*Dorosoma cepedianum*). In contrast, banded sculpin was not found at the most downstream sites, a possible indication of temperature restriction (Appendix 1).

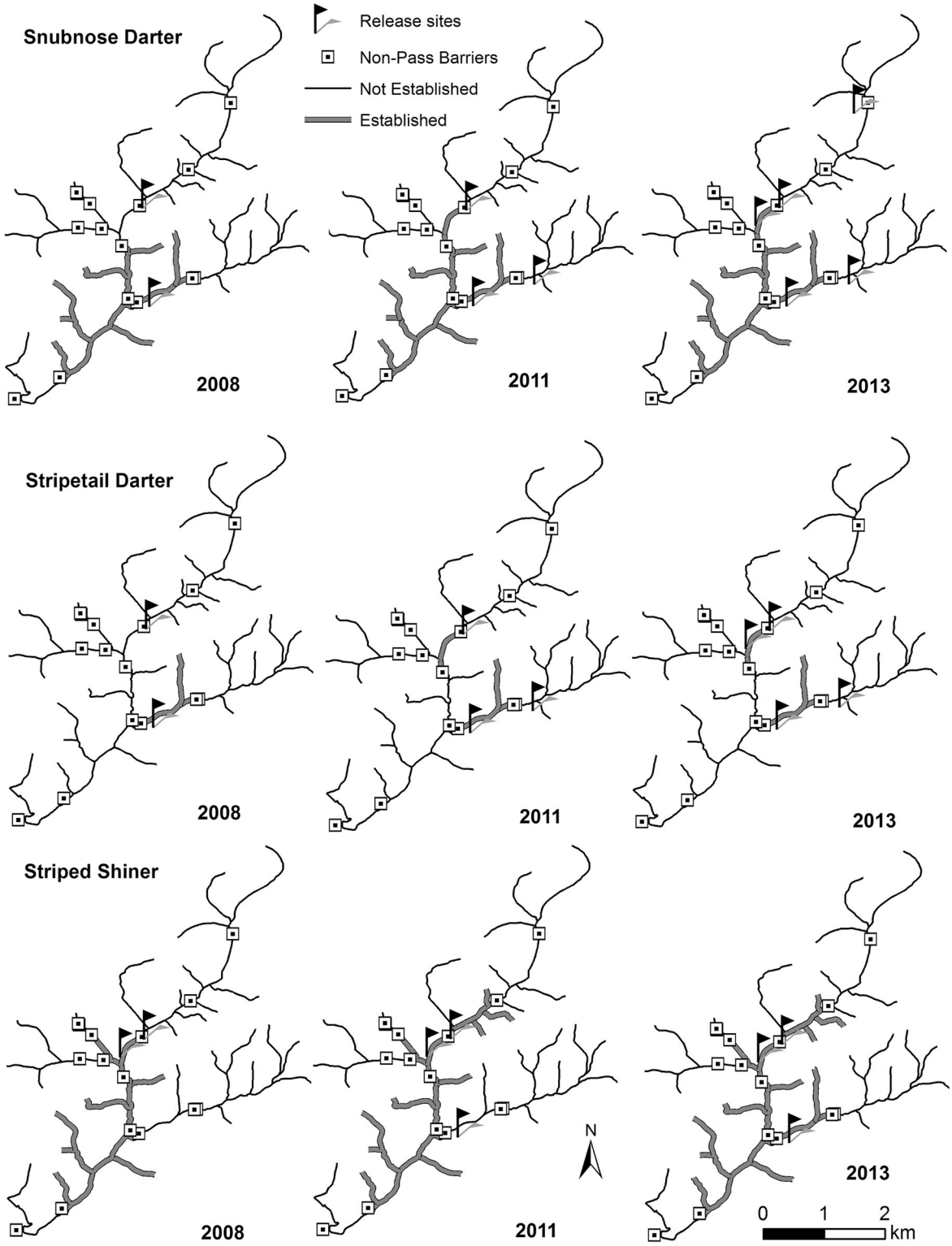
Barriers, fragmentation indices, and additional stressors

Within the WOC watershed, we identified 31 barriers, of which 14 were impassable, 6 were fully passable, 6 were partially passable (to shiners), and 5 had insufficient information (Fig. 1). Fish community sites varied considerably in their fragmentation indices and stressor metrics (Table 1). Strong correlations were observed within and among fragmentation index groups. Positive correlations among barrier scenarios (all, pp, and np) were present for fragment lengths (FL), dendritic connectivity index (DCI), and barrier index (BI) (Spearman's rho = 0.62–0.96, $P < 0.05$). Outfalls were not correlated with fragmentation indices or watershed position.

Ecological recovery and fragmentation

Species distributions—Following introduction, species dispersal remained within the reach of release or in the downstream direction and never occurring above impassable barriers (Fig. 3, Supplementary Material 1). In addition, some upstream movements did not occur in tributaries blocked by partially passable barriers or barriers with insufficient information (partially passable barriers not displayed in Fig. 3). Striped shiner showed the greatest dispersal, including the most upstream movements below barriers (Fig. 3). Populations failed to successfully establish for snubnose darter and stripetail darter in some locations; however, striped shiner established populations in all introduction locations.

Trends in richness and biomass—Across the study period, increases in species richness occurred within the watershed; however, this pattern was not observed at all sites (Fig. 2). Prior to species introductions (1987–2007), 8 of the 11 sites had negative site*year coefficients (Fig. 4). When considering all years (1987–2013), five of the sites had negative site*year coefficients for richness, all but one of which was negative for the pre-2007 models. Four sites had negative site*year coefficients for biomass in the pre-


Release sites
Non-Pass Barriers
Not Established
Established
Snubnose Darter
2008
2011
2013
Stripetail Darter
2008
2011
2013
Striped Shiner
2008
2011
2013
N
0
1
2
km

◀**Fig. 3** Spatial distribution of three of the six introduced species over time within White Oak Creek watershed with regard to non-passable barriers following introductions. Establishment suggests that adults were found in increasing numbers more than one year or young-of-year were present. Results for other species are provided in Supplementary Material 1

2007 model, whereas five sites had negative coefficients for biomass in the all-years model (Supplementary Material 2). In general, species recovery was negatively related to the degree of fragmentation. Coefficients for richness models were positively

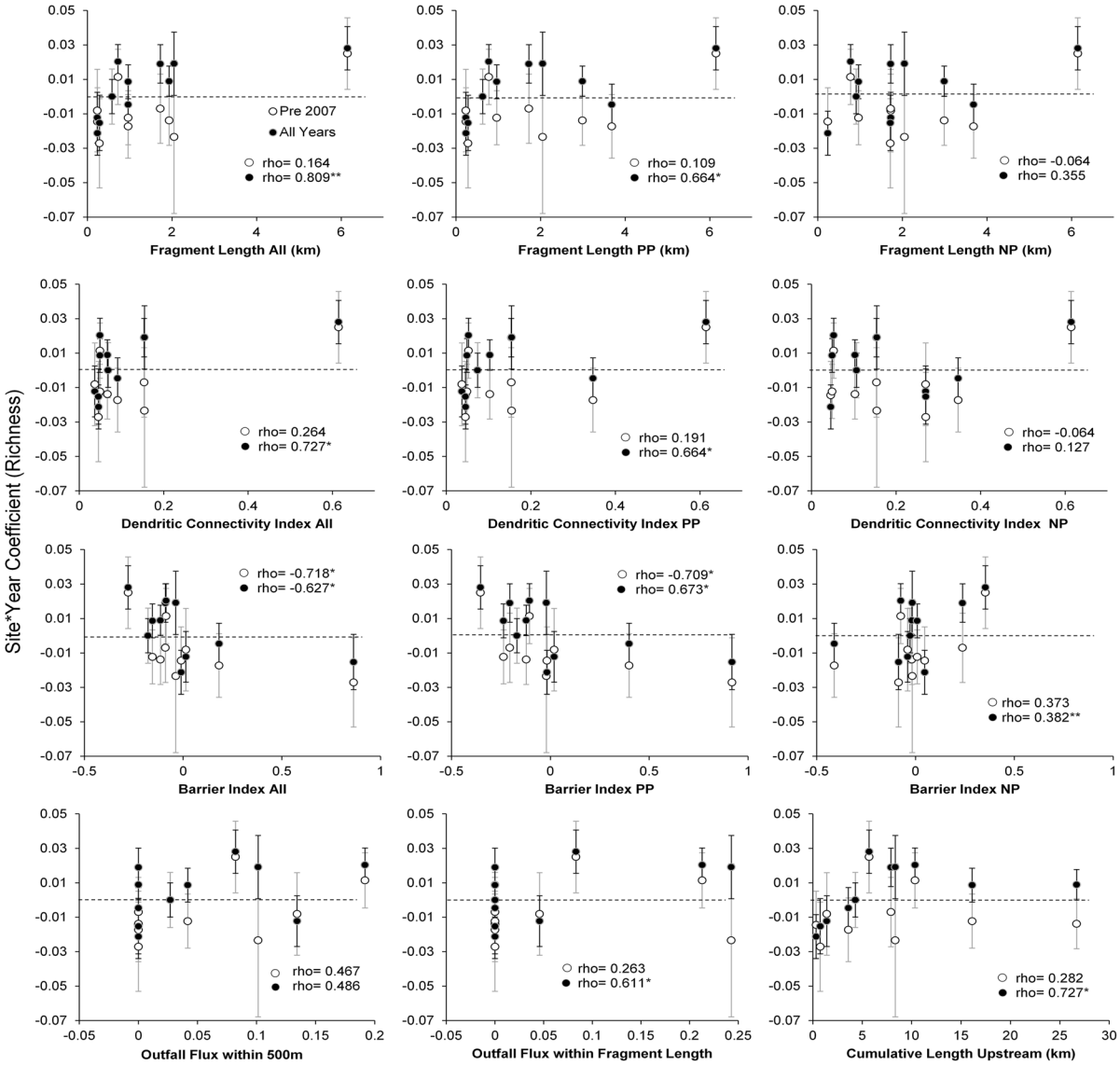


Fig. 4 Ecological recovery in species richness relative to fragmentation indices and outfalls. Site*year coefficients were calculated from generalized linear mixed models predicting richness over time using only observations prior to 2007 and then observations for all years (to account for introductions). Spearman's rank correlation coefficients (rho) were used to examine the strength of relationships between each metric and site*year coefficients. *Error bars* represent 1 SE. *, **, and *** indicates statistical significance of correlations at the 0.05, 0.001, and 0.0001 levels, respectively

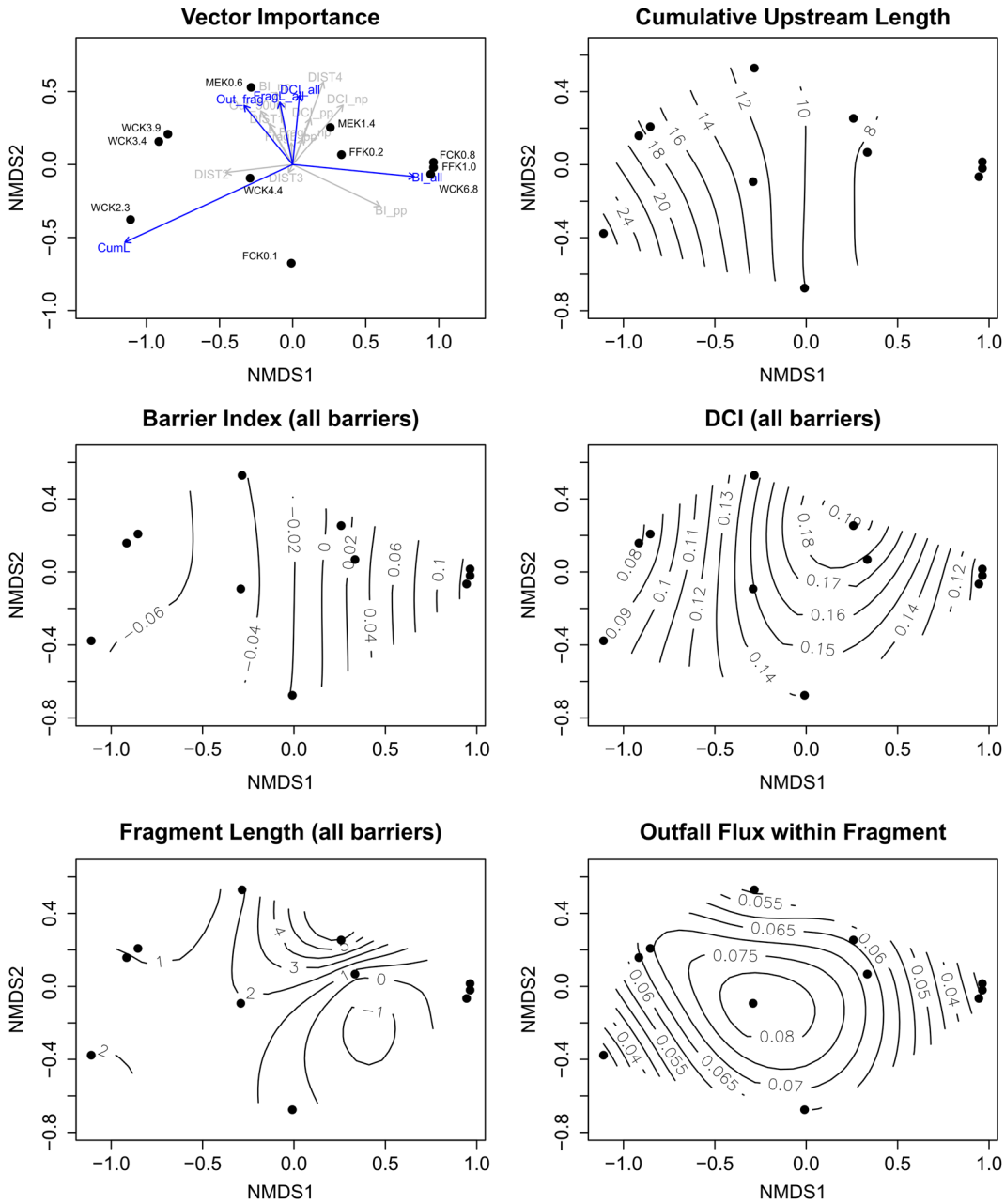


Fig. 5 Example of Non-metric Multidimensional Scaling ordination of fish community sites for spring 2013 and vectors (explanatory variables) fit to the ordination space. *Vectors* in *blue* represent variables used to create smooth surfaces (splines) of environmental gradients among sites, whereas *gray vectors* represent all other explanatory variables

correlated with fragment lengths and DCI and negatively related to barrier index (Fig. 4). Typically, fragmentation indices calculated for all barriers showed the strongest correlations compared to those for partial barriers and non-passable barriers. In addition, correlations for all years were stronger than correlations for only pre-2007 years. Strong correlations were not apparent for biomass coefficients and fragmentation indices (Supplementary Material 2). Out_frag was positively correlated with richness coefficients, but neither of the water quality metrics was related to biomass coefficients.

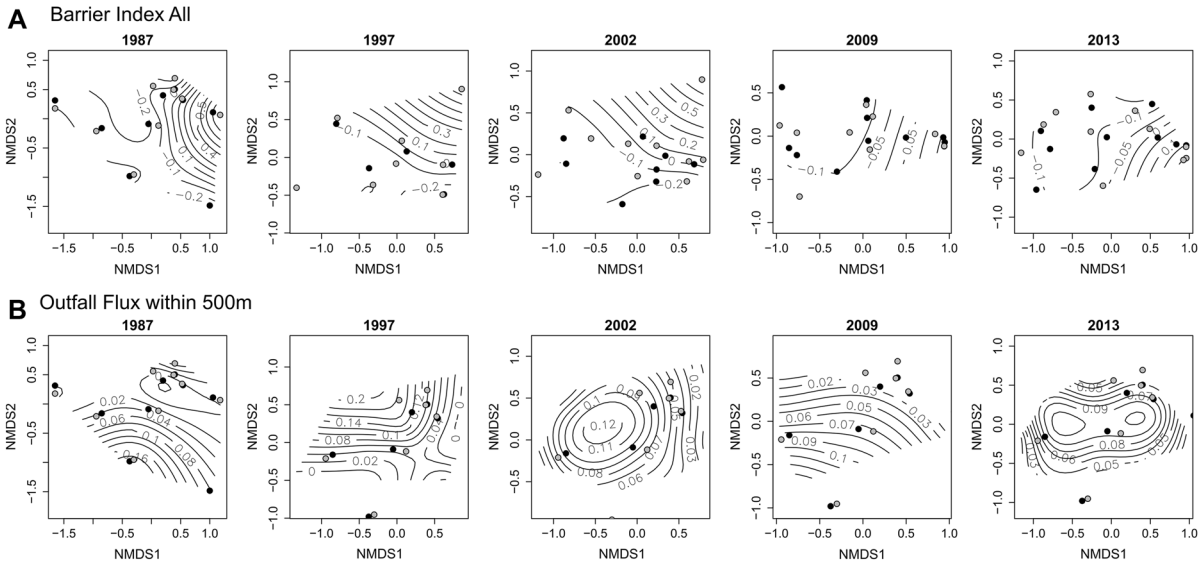


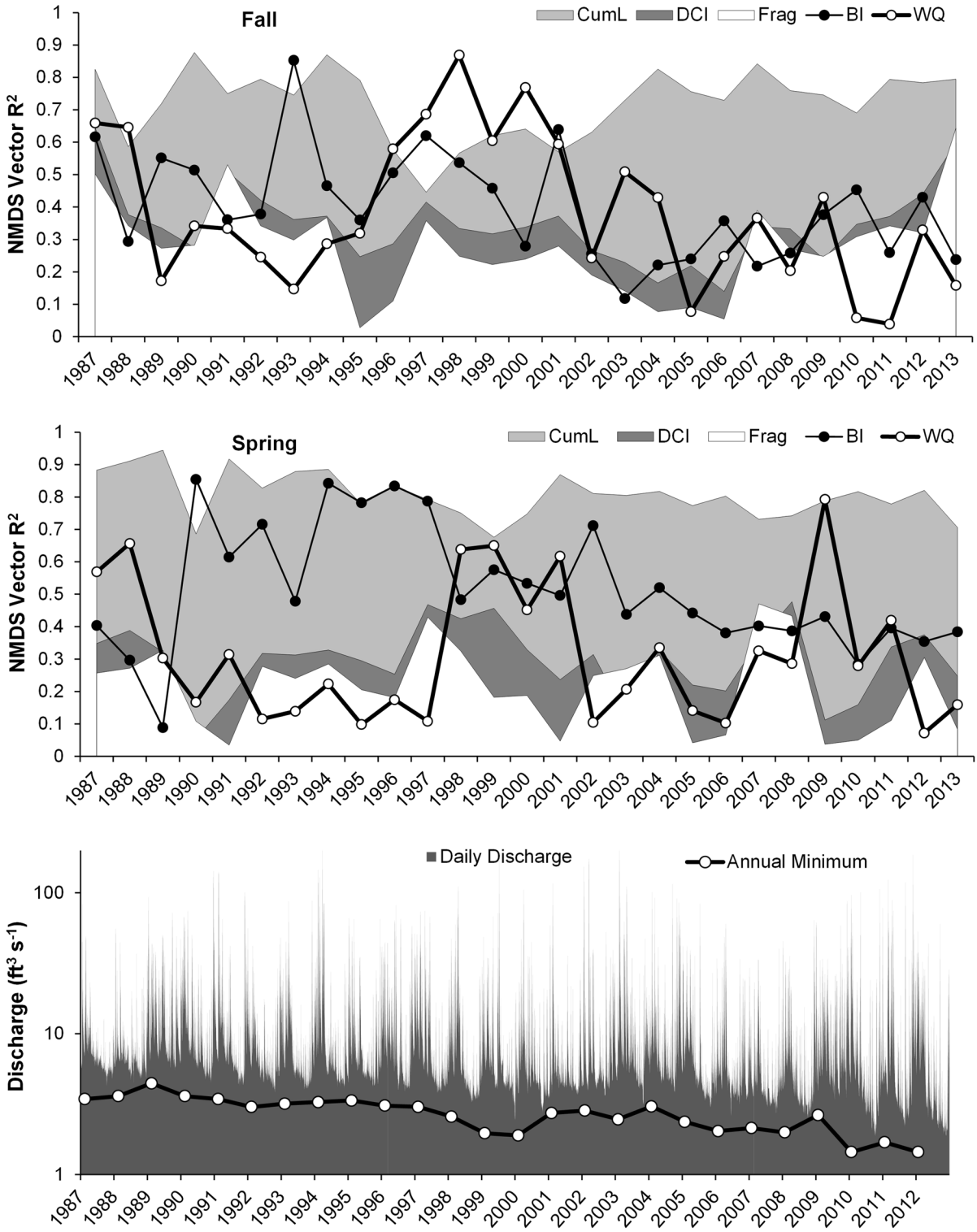
Fig. 6 Temporal variation in fish community ordination space with regard to season and smooth surface splines for **A** barrier index_all and (**B**) outfall flux within 500 m. *Black dots* = fall, *gray dots* = spring

Trends in fish community composition—Trends in community composition were apparent among sites (Fig. 5) and among seasons (Figs. 6, 7) according to position within the watershed, fragmentation, and outfalls. Typically, communities showed greater variation during spring seasons, thus creating a larger gradient for explanation by environmental variables (Fig. 6). Temporal changes in community composition were also apparent as evidenced by variation in vector importance (Fig. 7); however, vector importance seemed unrelated to species introductions. Cum_L and DIST1 (the first distance eigenvector) consistently explained the most variation in fish communities, followed by BI_pp, BI_all, and DCI_np (Fig. 7; Supplementary Material 3). The importance of CumL tended to show less variation across time, whereas BI indices and water quality showed considerable variation (Fig. 7). However, the importance of CumL in the spring displayed significant declines over time (rho = −0.46, $P = 0.019$). Fragment length and DCI indices tended to explain less variation; however, vector strength fluctuated among years.

The importance of BI indices was typically stronger in the spring than the fall (Figs. 6, 7, Supplementary Material 3); however, for both seasons, R^2 values steadily decreased over time (rho = −0.50, $P < 0.01$) with a conspicuous decline in values and variation in values after 2002 (Figs. 6A, 7). Prior to 2002, vector importance for BI indices peaked during several instances in the fall and spring seasons. Water quality indices R^2 were variable and did not show consistent trends over time; however, several intermittent periods were characterized by high values (Figs. 6B, 7).

Stream flow magnitudes showed consistent declines across the study period (annual minima, rho = −0.87, $P < 0.0001$; annual average, rho = −0.44, $P = 0.025$) (Fig. 7). Although strong correlations been flow statistics and vector importance were not observed, significant correlations between flow and BI indices were more numerous than other metrics (Supplementary Material 4). Vector strengths for BI were typically positively correlated with flow magnitudes, regardless of season (>0.50, $P < 0.05$; Supplementary Material 4). Out_frag vector R^2 was negatively correlated with stream flow magnitudes only during the spring and only during 1- and 2-year time lags.

Fish assemblages in WOC were dominated by equilibrium strategists; however, less isolated sites showed more life history diversity with increasing periodic and opportunistic species (Fig. 8). Variation in life history composition among sites and among years was far greater at less isolated than highly isolated sites. Isolated sites showed far more


Fall
CumL
DCI
Frag
BI
WQ
NMDS Vector R2
Spring
Daily Discharge
Annual Minimum
Discharge (ft3 s-1)

◀**Fig. 7** Temporal variation in the importance of environmental vectors explaining variation in fish communities as measured by R^2. R^2 values represent the maximum value for all indices within a group (e.g., Barrier index represents maximum value for BI_all, BI_pp, BI_np). Ordination was conducted for each site for each year. *Bottom panel* shows daily stream discharge and annual minimum discharge across the study period, measured at the center of the watershed

domination by equilibrium species with site concentrated on the equilibrium-opportunistic (E-O) plane near the equilibrium endpoint (Fig. 8). No periodic species were observed at highly isolated sites except FCK0.8, where the assemblage moved from the equilibrium-periodic (E-P) plane to the E-O plane over time due the disappearance of largemouth bass. Less isolated sites displayed homogenized life history diversity over time with consistent shifts towards the equilibrium endpoint and E-O plane.

Discussion

Given the extent of pollution abatement and water quality remediation efforts, our results suggest that barriers in the White Oak Creek watershed are a major factor limiting the full potential of fish community recovery by impeding fish dispersal and recolonization. However, isolating the true role of dispersal on

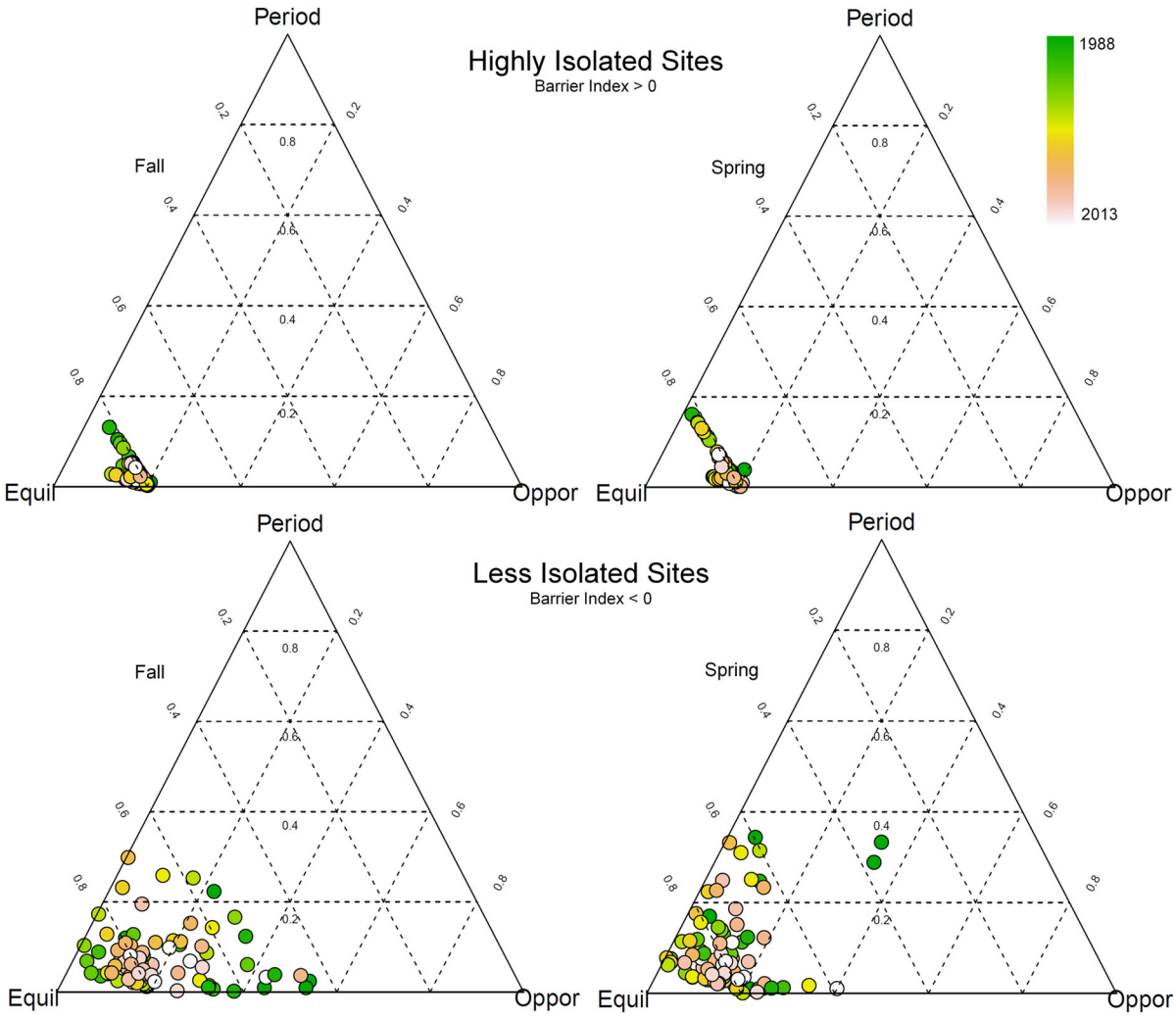


Fig. 8 Ternary plots of the tri-point life history composition of fish assemblages at sites according to degree of isolation, season, and year. Temporal trends were based on fish assemblage sampling at each site every other year from 1988 to 2013. *Equil* equilibrium, *Oppor* opportunistic, *Period* periodic

limiting ecological recovery is complicated due to the compounding effects of other disturbances still at play in the watershed. Sites isolated by barriers displayed little or no increases in species richness over 26 years, whereas gross increases in richness were more evident at sites connected to more habitat patches. The negative effects of barriers on fish community recovery were further substantiated by observations of fish species dispersal. Following introductions, upstream passage above barriers by all six species was never observed.

When interpreting our results, there are several factors that should be taken into consideration. Relative to other watersheds, WOC is extremely fragmented, with 1.85 barriers/km^2 compared to 0.03–0.392 barriers/km^2 reported for other studies (Meixler et al., 2009; Favaro et al., 2014). In addition, our analysis was conducted at a relatively fine spatial scale, i.e., among sites within the WOC drainage. At a broader scale, the WOC watershed is disconnected from the Clinch River system by two large dams in the lower watershed; hence, the entire WOC drainage is disconnected from sources of colonists and migrants as evidenced by considerably fewer species than neighboring watersheds. For example, Bear Creek, a neighboring watershed with similar size (19.6 km2) to WOC, has an unobstructed migratory corridor to the Clinch River. Despite having disturbances comparable to WOC, Bear Creek has ten more native species. Thus, the effects of barrier isolation on ecological recovery at some sites should be considered with regard to the fact that all sites within WOC, to some extent, are isolated.

While trends in richness displayed intuitive relations to habitat fragmentation, the positive correlation between outfall flux within fragments and fish community recovery was unexpected. This potentially suggests that areas with the most significant water quality issues have dramatically improved from remediation actions; however, this should not suggest that water quality is not still a potential limiting factor in fish community recovery. Chronic and acute stressors, such as high water temperatures and episodic surges of chlorinated water, respectively, are still at play within WOC, both of which have lead to fish kills. One difficulty in isolating the effects of poor water quality conditions is that contaminants and effluents may have pervasive effects across much of the watershed from historical activities. Secondly, the outfalls we identified were classified as 'significant' due to their role as being primary sources of historical contaminant and effluent levels; however, there are a considerable number of outfalls on the ORNL campus, and any one of which could periodically contribute to poor water quality conditions. Although water quality conditions have dramatically improved since the 1980s, legacy and episodic water quality disturbances are likely also limiting community recovery.

Observed patterns in life history composition among sites were in accordance with that predicted by life history theory. As predicted, highly isolated sites were almost entirely composed of equilibrium strategists and displayed less variation in life history composition over time. In contrast, communities at less isolated sites contained periodic and opportunistic species and showed more variation in life history composition among sites and over time. In general, all sites displayed homogenization in life history diversity with time towards the equilibrium endpoint along the equilibrium-opportunistic plane, regardless of the degree of isolation. In part, this was likely due to the dispersal of introduced species at less isolated sites, the majority of which were equilibrium or equilibrium-opportunistic strategists.

In contrast to richness, isolating causal mechanisms behind community composition dynamics over time was difficult. The importance of barriers and outfalls on fish community composition varied across seasonal and annual periods and was potentially related to a combination of streamflow, pollution abatement programs, remedial actions, and episodic disturbance events within the watershed. Contrary to our hypotheses, barrier index explained more variation in fish community composition during higher flow conditions (e.g., Spring), a possible indication of seasonal migration by some species at non-isolated sites. In addition, the effect of barriers on fish community composition displayed declines over the entire study period, which correlated with consistent decreases in streamflow magnitude. However, we suspect that this may only be correlation as opposed to true causation, as communities are recovering and becoming more stable and homogenous with time. As an alternative explanation, the decline in the importance of physical barriers may be related to the progressive improvement in water quality conditions across WOC.

Dispersal theory and restoration effectiveness

The theory of dispersal mechanisms limiting the ecological effectiveness of restoration efforts has seen wider attention related to terrestrial communities (Marzluff & Ewing, 2001; Schrott et al., 2005; Brudvig et al., 2010) than aquatic communities (Miller & Hobbs, 2007; Brederveld et al., 2011). We distinguish restoration studies from studies assessing recolonization following major disturbances, which are far more abundant in the aquatic literature (e.g., Kubach et al., 2011; Erős et al., 2015). Indeed, the negative effects of in-stream barriers on fish populations and communities have been widely addressed (Warren & Pardew, 1998; Perkin & Gido, 2012). Likewise, in-stream barrier removals have become frequent restoration projects (Hitt et al., 2012), including regional prioritizations of barriers on slate for future removal (Kuby et al., 2005; Kocovsky et al., 2008; Perkin et al., 2015). Barrier removals provide excellent controlled experiments to directly measure the importance of dispersal limitations on fish communities (Hitt et al., 2012). In contrast to controlled restoration experiments, analyses assessing existing habitat fragmentation effects on fish assemblages may not fill a fundamental knowledge gap in dispersal limitations unless there is consideration of barrier permeability (Pépino et al., 2012) and other potential constraints, such as landscape condition (Mahlum et al., 2014b) or intrinsic population characteristics, such as small population size (Fraser et al., 2014) or vulnerability to extinction (Schrott et al., 2005). Furthermore, prioritizing barriers for removal requires many assumptions about the potential for improving ecological conditions, and many fish-related studies have not considered whether habitat availability is, in fact, the limiting factor (Kuby et al., 2005).

We found that ecological recovery was more related to the degree of isolation of local communities by barriers within the WOC watershed, as opposed to a measure of fragmented stream length, *per se*. In other words, the combination of the location of the community within the watershed (e.g., headwater, mainstem) in relation to fragmentation was the main driver of dispersal limitation. We make this distinction because the entire watershed is highly fragmented; thus, relative differences among communities are viewed in light of their position and connectivity to other patches. For example, the fish community at upper First Creek (FCK0.8) has seen little change in species richness since 1987 despite being the focal point of riparian restoration and sediment reduction (Fig. 2). In comparison, richness has doubled in lower First Creek (FCK0.1), only 700 m downstream (Fig. 2). The difference in ecological recovery cannot be attributed to total fragment length as both have very short free-flowing distances between barriers (Table 1). Alternatively, FCK0.1 has experienced more recovery because of having open access to another tributary and the WOC mainstem, both of which were within close proximity (Fig. 1). Similarly, Kubach et al. (2011) found that recovery rates in fish assemblages following a major oil spill depended on proximity and connectivity to sources of colonists. As another example, the BCK watershed has more species than WOC due, in part, to its connection with other species pools (e.g., Clinch River, East Fork Poplar Creek) and not necessarily the total length of unobstructed habitat.

We also found that the effect of barriers on ecological recovery was stronger when considering years after post-species introductions. Species successfully established at release sites or in areas where they could colonize by swimming downstream across barriers, but failed to colonize at the most isolated sites. Furthermore, ecological recovery was also related to species-specific recolonization potential, which was partially a function of swimming ability. Using an experimental analysis, Albanese et al. (2009) found that movement potential was related to a fish's ability to colonize new areas and was unrelated to body size. Similarly, in our study, striped shiner had the strongest swimming ability and displayed the greatest dispersal in WOC, but was not among the largest species. Rock bass, a poor swimmer, did not disperse beyond release sites in the lower watershed and failed to establish at other introduction locations (Supplemental Material 1). Northern hog sucker, however, has moderate swimming and leaping ability (Meixler et al., 2009), but yet also showed minimal dispersal beyond release sites. Thus, another consideration is whether sufficient habitat, such as pool depth, is present to support establishment.

In contrast to mobility-related traits, life history theory proved a useful template for evaluating fish community responses to long-term restoration. However, Erős et al. (2015) found that life history theory did not successfully predict fish assemblage recolonization dynamics following a large-scale disturbance.

In contrast, they found that the occurrence and abundance of fish species in the watershed, as opposed to traits, were the best predictors of colonization. Similarly, Kubach et al. (2011) found that species abundance, in conjunction with barriers, influenced recovery potential at sites following disturbance. Possibly, one difference in our study to those of recolonization studies was the continued presence of the disturbance gradient (i.e., barriers and water quality), which would continue to structure fish assemblages according to life histories. In addition, because of the presence of major dams at the outlet of the watershed, new species were introduced in WOC as opposed to natural recolonization.

We speculate that isolation by barriers in conjunction with episodic releases of toxicants or effluents high in dissolved salts or temperature are still influencing fish communities in WOC by impeding escapement into areas of refugia. However, isolating the true mechanisms by which existing water quality concerns are influencing communities is difficult due to the large number of disturbances that are still pervasive and not just present within fragmented reaches. Evaluating the role of the combined effects of barriers and poor habitat conditions is an important area of research related to dispersal limitations and restoration science. For example, Perkin et al. (2015) documented the compounding role of dewatering and habitat fragmentation on the decline of endemic minnows in streams of the Great Plains, USA. Hence, the importance of barriers, or lack thereof, must be viewed within the context of existing landscape conditions (Mahlum et al., 2014b), in order to prioritize restoration objectives.

Temporal dynamics of dispersal limitation on communities

Besides the location of sites within the watershed, our results suggest that the presence of barriers (i.e., based on BI), on average, was the strongest factor affecting fish community composition, suggesting that isolation played a significant role in controlling the immigration of seasonal migrants and fluctuations in the abundance of a few, dominant species (e.g., largescale stonerollers, blacknose dace). However, the importance of BI declined throughout the period with values remaining low and stable post-2002. Although the importance of BI correlated with streamflow magnitudes, we believe that this relationship is correlative as opposed to causative for the following reasons. As several pollution abatement projects were completed through the 1990s (Fig. 2), artificially high discharges have progressively decreased. Declines in barrier importance are also likely due to several interacting factors linked to the recovery and stabilization of community dynamics over time, with 2002 bearing no significance other than the transition into a new successional stage of community recovery (Beisner et al., 2003). At highly isolated sites, communities have remained dominated by a few individual equilibrium species. However, newly introduced equilibrium and equilibrium-opportunistic strategists have homogenized the composition of less isolated sites, lessening the degree of divergence among sites within the watershed. Hence, communities have become more stable and homogenized over time with a noticeable shift towards the equilibrium endpoint along the equilibrium-opportunistic plane. While barriers appear to be playing an important role in shaping the temporal dynamics of fish communities within WOC, the extent to which cumulative disturbances and environmental barriers are individually or interactively driving community patterns is still unclear.

Conclusions

Similar to other studies (Kubach et al., 2011), our study provides strong support of dispersal limiting fish community recovery. Barriers to dispersal were playing a role in limiting fish community recovery to pollution abatement and water quality remediation in WOC by preventing colonization from introduced species and seasonal migrants. Our analysis shows that measures of isolation, such as barrier index, and the location of barriers may be more important in describing fish community dynamics than traditional fragmentation metrics, such as fragment length, because measures of isolation place barriers in the context of sources of colonists while controlling for spatial proximity. Long-term monitoring provided an opportunity to assess the effectiveness and limitations of restoration actions; however, isolating the relative importance of physical barriers compared to other factors, such as existing water quality conditions, in fish community recovery is difficult, especially in watersheds where multiple stressors are acting

simultaneously. Thus, more research is needed to fully understand the role of dispersal in restoration ecology and its interaction with other landscape disturbances.

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