Canadian Journal of Fisheries and Aquatic Sciences

Evaluation of the Influences of Dam Release Types, Land Use, and Habitat Affecting Abundance, Richness, Diversity, and Community Structure of Larval and Juvenile Fish

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2017-0107.R3
Manuscript Type:	Article
Date Submitted by the Author:	11-Sep-2018
Complete List of Authors:	Hanks, R.; Clemson University, Department of Forestry and Environmental Conservation Hartman, Kyle; West Virginia University
Keyword:	DAMS < Environment/Habitat, FRESHWATER < Environment/Habitat, STREAMS < Environment/Habitat, BIODIVERSITY < General, HABITAT < General
Is the invited manuscript for consideration in a Special Issue? :	Not applicable (regular submission)

SCHOLARONE™
Manuscripts

Title: Evaluation of the Influences of Dam Release Types, Land Use, and Habitat Affecting
Abundance, Richness, Diversity, and Community Structure of Larval and Juvenile Fish

Authors:

R. Daniel Hanks^{1,2} and Kyle J. Hartman*
West Virginia University, Department of Wildlife and Fisheries Resources,
310A Percival Hall, Morgantown, WV, 26506, USA

Footnotes: ¹Corresponding author (e-mail: rhanks@clemson.edu, phone: 864-200-8167)
²Present address: Department of Forestry and Environmental Conservation, Clemson University,
118A Lehotsky Hall, Clemson, SC, 29634, USA
*e-mail: hartman@wvu.edu

Abstract

We systematically evaluated the influence of dams on downstream aquatic habitat and early life stage (ELS) fish at two spatial scales from epilimnetic and hypolimnetic discharges and made comparisons to a control stream. ELS fish exhibited a general increase in abundance, richness, and Shannon diversity with increasing distance from dams in both epilimnetic and hypolimnetic release types. Nonmetric multidimensional scaling (NMDS) indicated larval and juvenile fish communities were structured differently between epilimnetic and hypolimnetic releases and habitat variables structuring those communities were more variable in epilimnetic releases than hypolimnetic releases. Rapid changes occurred within the first 1,100-m reach and a second more gradual gradient extended beyond the 5,100-m sample reach. Generally, our findings agreed with that of the Serial Discontinuity Concept (SDC) but we believe future studies should be explicit in the systematic evaluation of the SDC and further studies are required to understand the two recovery gradients that exist below impoundments.

Introduction

River ecosystems are often conceptualized as continuous entities along their longitudinal gradient. At large scales where such a concept may be applicable, the River Continuum Concept (RCC) proposes that the physical and chemical features continually change along the stream gradient from headwaters to sea; thereby structuring the associated biological communities (Vannote *et al.* 1980). Scale refers to the extent relative to the size of the sampling unit of a variable of interest in both space and time (Schnieder 1989; Weins 1989). As scale is reduced, these changes become less prominent and may not appear to follow the RCC but rather seem somewhat random (Ward *et al.* 2001).

Due largely to anthropogenic influences, the majority of lotic ecosystems no longer act as continuous entities and instead are influenced by discontinuities along their longitudinal gradient (Ward and Stanford 1983), of which dams are likely the most influential. The Serial Discontinuity Concept (SDC) (Ward and Stanford 1983) created the theoretical framework to understand how discontinuities modify physiochemical and biological components upstream and downstream of dams. Where free-flowing lotic systems exhibit continuous changes along their longitudinal gradient that fit the RCC model, the SDC is a model to understand how dams disrupt those biological, chemical, and physical changes. These disruptions can result in abrupt modification to the physicochemical and biological attributes making the system similar to a stream reach either further upstream or downstream, depending on dam location along the stream gradient. Physiochemical changes associated with dams have been shown to adversely influence biological components (e.g., fish, aquatic macroinvertebrates, etc.) of stream communities (Ellis and Jones 2013; Freedman *et al.* 2013; Katano *et al.* 2009). Discontinuities within a stream can reset or shift a variable in either the upstream or downstream direction (Ward and Stanford

1983). The size, relative location of dams along the length of a stream, and type of release (epilimnetic or hypolimnetic) may have differential effects on downstream physiochemical and biological attributes (Yeager 1993; Ward and Stanford 1983) and should be considered when evaluating a dam's impact on the abiotic and biotic components of that system. In order to further understand the nature of biological recovery gradients along these longitudinal discontinuities, empirical approaches are necessary (Stanford and Ward 2001).

Numerous studies have examined abiotic and biotic components below dams and compared them to expectations of the Serial Discontinuity Concept (SDC). Most have found results to generally agree with the theoretical construct of the SDC (Ward and Stanford 1983). In a review of studies on nine rivers, Stanford and Ward (2001) found only one in which the SDC did not hold up—attributed to eutrophication and salinization downstream. Animal taxa apparently showing recovery gradients below dams include invertebrates, anurans, and fish. Among benthic macroinvertebrate studies, Plecoptera are typically reduced below dams and Trichoptera are enhanced with these trends diminishing with distance from the dam (Ellis and Jones 2016). Guzy *et al.* (2017) found anuran occupancy and species richness increased with increasing distance downstream of dams presumably due to altered flow regimes reducing riparian breeding habitat.

Many studies have demonstrated the influence of dams on downstream habitat (Harvey 1987; Katano 2003; Thompson 2011). Dams have been demonstrated to disrupt sediment transport, resulting in reduced downstream sediment loads, modify sediment composition, armoring of streambeds, and erosion of stream banks (Jones, 2010). Substrate size and velocity are often altered at sites in close proximity to dams, where substrate is often larger and velocity higher than expected were dams absent (Freedman *et al.* 2013; Katano *et al.* 2009; Cortes *et al.*

2002; Poff and Hart 2002; Graff 1999; Storey *et al.* 1991). Shifts in thermal regimes can be a product of impoundments and the magnitude of change above and below the dam is dependent on whether the dam release is hypolimnetic or epilimnetic. Epilimnetic surface releases are typically well oxygenated with temperatures near ambient but can result in elevated temperatures in the summer and winter and delay in warming and cooling of waters released downstream (Fraley 1968). Reservoirs may become stratified and where dams release water hypolimnetically the reduced water temperature may be as much as 13-18 °C (TVA 1978). Both epilimnetic and hypolimnetic releases have been shown to negatively impact biota (Yeager 1993). The rate at which temperature changes as the distance from dam increases is dependent on multiple factors (e.g., the number, size, and temperature of tributaries, latitude, canopy cover, etc.) (Rice *et al.* 2001). Dams may influence water quality, which is known to structure biotic communities (Storey *et al.* 1991; Freedman *et al.* 2013).

Land use practices have been shown to influence aquatic ecosystems (Allan 2004) in regard to both their biotic and abiotic components (Roy *et al.* 2003; Allan and Johnson 1997 Johnson *et al.* 1997). Johnson *et al.* (1997) found agricultural land use to be an effective predictor of water chemistry variables in central Michigan's Saginaw River basin. Urbanization and forested land cover had opposite effects on various benthic invertebrate biotic indices, with higher values associated with forested areas; whereas urbanization resulted in higher proportions of tolerant taxa and reduced diversity (Roy *et al.* 2003). Within the context of the SDC, land use practices should be considered as potentially influential in structuring water quality, habitat, and biotic indices and may do so in a cumulative fashion.

Adult fish and aquatic macronivertebrates, of river ecosystems in the context of the SDC have been largely studied (Rice *et al.* 2001; Cortes *et al.* 2002; Ellis and Jones 2013); yet there

have been few studies to evaluate dam influences on larval and juvenile fish (Song *et al.* 2018), where early life stage fish serve as surrogates for successful fish reproduction. During these early portions of fish's life cycle they have little ability to move substantial distances and are likely found in close proximity to the location where their parents spawned. Additionally, any movement is likely downstream as they enter the drift for dispersal purposes (Webb 1975). There has been a lack of true of efforts to understand the response of early life stage fish to impounded systems and the cumulative effects of land use and in stream habitat along the longitudinal gradient below dams. As such, the objectives of this study were to systematically: 1) evaluate changes in abundance, richness, and diversity along the longitudinal gradient below dams in both epilimnetic and hypolimnetic releases in comparison to a control stream; 2) investigate how habitat (in stream, land cover, and water quality) influences richness and diversity along the longitudinal gradient of impounded streams; 3) investigate drivers that structure fish communities within both epilimnetic and hypolimnetic dam releases and a control stream. We hypothesized, concurrent with the SDC, that the aforementioned response variables, community structure, and changes in habitat will show a strong relationship with increasing distance from dams.

Materials and Methods

Study Sites

Sampling occurred during 2012 and 2013 in six dammed streams (three each of epilimnetic and hypolimnetic) and one control stream (Figure 1). All streams were located in the mid-Atlantic region of the United States (Figure 1) and were transitional cool water systems except Big Walnut Creek, Ohio, USA which was a warm water system (Sheldon *et al.* 2015). In 2012 we sampled the Savage River, Maryland, USA but were unable to replicate sampling in

Savage River during 2013 due to permitting issues with Maryland Department of Natural Resources. Savage River was replaced in 2013 with East Branch of the Clarion, PA. New Creek, West Virginia, USA was selected as a control stream based on prior work (Hanks 2016) and work by Niles and Hartman (2007) within the region and thus knowledge of the system as being representative of a reference condition within the central Appalachian region.

Sixteen sampling sites per stream were selected *a priori*. In dammed streams, the uppermost sampling site was located immediately below the respective dam, while in our control stream, the uppermost site was located approximately 14-km downstream of the nearest upstream dam. Of the 16 sites per stream, the first seven were spaced 100-m apart and the remaining nine sites were spaced at 500-m intervals (Figure 1C and Figure 2). Preliminary data (Hanks unpublished 2011) suggested very low taxa richness within the first 600-m below the dam and thus we used the finer spatial scale to identify the distance downstream of dams where larvae and juveniles were first found. To assess the discontinuity distance associated with each dam, our most downstream sample site was 5,100-m below the respective dam.

Sampling methodology

Larval and juvenile fish were sampled twice in each of 2012 and 2013 between mid-May and mid-June at each of the 16 sampling sites per stream during daylight hours (0900-2000). Our prior sampling for larval and juvenile fish (Hanks unpublished data) and work by Niles (2004) indicated high numbers of individual larvae and juveniles captured and high taxa richness in these months in this region. At each sampling site, fish were sampled with small aquarium dip nets (12-cm x 15-cm; mesh size = 500- μ m) a total of 25 minutes (five distinct five-minute periods) using a modified sweep net technique (Hanks 2016). This modified sweep net technique is an adaptive cluster sampling technique (Greenwood and Robinson 2006) where

personnel wade the stream while looking for larval and juvenile fish. Once fish are seen they are swept into the net (Hanks 2016). Captured fish were washed into sample jars, labeled, and preserved with 10% buffered formalin (Kelso *et al.* 2013). Larvae were returned to the lab for identification.

Water quality variables (conductivity ($\mu\text{S}/\text{cm}$), dissolved oxygen (mg/L), pH, and temperature ($^{\circ}\text{C}$)) were recorded concurrent with larval and juvenile fish sampling at each sample site with a YSI meter (Yellow Springs Instruments computer module: 650MDS). The physical habitat variables channel and bankfull width were measured at five transects spaced 5-m apart per sample site. Depth, flow, percent embededness, and substrate were measured at five point locations along each of the five transects per sampling site (Figure 2). Flow measurements were recorded with a Marsh-McBirney flow meter (Marsh-McBirney Inc., Frederick, Maryland). Substrate were coded based on size class categories as follows: 1 = bedrock (>4000 mm), 2 = fines (<0.06 mm), 3 = sand (0.06-2 mm), 4 = fine gravel (2-16 mm), 5 = coarse gravel (16-64 mm), 6 = cobble (64-250 mm), and 7 = boulder (250-4000 mm). Average substrate coarseness (Katano *et al.* 2009) at each sampling site was used in models and calculated as:

$$\text{Coarseness} = \Sigma (\text{Size category code} \times \% \text{ of a given category at a given transect})$$

Additionally, average substrate diversity (Shannon diversity) and overall habitat diversity (Shannon diversity for substrate, depth, and flow) was calculated for each site.

Landscape habitat variables

Using spatial analyst functions in ArcMap 10.2.1 (Environmental Systems Research Institute, Redlands, California) we generated watersheds for each sample site per each respective stream. Land cover (from the 2011 National Land Cover Dataset [NLCD]) types from each watershed were subtracted from the cumulative upstream watersheds in order to get the percent land cover type within each respective sub-watershed. Land cover types were then combined into three categories (developed, forested, and agricultural/grassland) for analysis. Road density (i.e., density = (road length/sub-watershed area) x 100) within subwatersheds was also calculated as a surrogate for development.

Laboratory processing of samples

All larval and juvenile fish samples were washed through a 500- μ m sieve and transferred to a dissecting tray. Using a Leica MZ6 dissecting microscope aided with a Cole-Parmer light ring and polarizing lens larval fish were identified to genus using various controls (Auer 1982; Holland-Bartels *et al.* 1990; Wallus *et al.* 1990). An advantage of the modified sweep net technique is that larvae are not damaged during the capture and fixation process and therefore we were able to identify all captured larvae.

Statistical analysis

We aimed to understand whether differences in response variables (i.e., abundance, richness, diversity, and community composition) between years and release types were significant. Therefore, we evaluated whether the changes in abundance, richness, and diversity along streams' longitudinal gradient were statistically significant between years and release types (i.e., epilimnetic, hypolimnetic, and control) with an ANCOVA. Statistical differences in community similarity along streams' continuum between years and release types were evaluated

using function Adonis in the program R (R Core Team 2016) vegan package (Oksanen *et al.* 2016). We also wanted to ensure that any differences in taxonomic richness were not due to drainage size. To assess if streams with larger drainage area had higher taxonomic richness (MacArthur and Wilson 1967), we regressed total generic richness on drainage area (mi^2) of each respective dam and total generic richness of each stream's 5,100 m stream reach for 2012 and 2013. We captured larval and juvenile fish during sampling; however, prior to analysis, all fish >30 mm in length were removed from the data set. Fish <30 mm in length were typically restricted to shallow stream margins and we reasoned that those fish would have had limited ability to move upstream in the systems we sampled relative to currents and hence, affect our estimates of displacement distance for a given taxa.

To understand how community structure changed along the stream continuum within each release type, we used nonmetric multidimensional scaling (NMDS) to summarize larval and juvenile fish community structure among sites based on genus-level abundance data (Bray-Curtis distance metric) using function metaMDS in the program R (R Core Team 2016) vegan package (Oksanen *et al.* 2016). Nonmetric multidimensional scaling is an ordination technique that plots sites based on similarities in multidimensional space, where sites plotting closer together are more similar (McCune and Grace 2002). Abundance data were $\sqrt{(x)}$ -transformed and Wisconsin double-standardized prior to analysis (Oksanen *et al.* 2016). To ensure a final convergent solution with the lowest possible stress, we used 20 random starts. Nonmetric multidimensional scaling solutions were determined in two through five dimensions; however, only the three-dimensional solution was used as stress was not reduced substantially in higher dimensions. We correlated individual community metrics and habitat variables with the ordination through vector fitting to determine the multivariate structure of the NMDS solution. Vector lengths are

representative of correlation strength to the ordination and distance represents the direction of most rapid change within the multivariate space. Individual stream sites were overlaid on the ordination to allow for investigation of community level changes that were associated with stream type, habitat, and distance from dam. Additionally, this approach allowed us to evaluate how each release type related to our control stream.

Habitat variables were correlated to the NMDS ordination to assess the relative influence of habitat changes on larval and juvenile fish community structure. Statistical strength (r^2) of the linear vector of each variable was determined with 1000 permutations using the envfit function in the program R (R Core Team 2016) package vegan (Oksanen *et al.* 2016). However, because linear interpretation of habitat variables is not always appropriate we also used generalized additive models to fit variables with thin plate splines in 2 dimensions (Wood 2003; Oksanen *et al.* 2016). Model complexity was determined via cross-validation to select the degree of smoothing and we used the coefficient of determination (r^2) to assess the significance of 1,000 permutations. This approach allowed us to evaluate whether variables in the NMDS solution responded in a linear or curvilinear fashion, depending on which method had the higher r^2 value (Oksanen 2016). This permitted us to evaluate the strength of relationships between habitat variables and fish community structure and whether communities responded in a linear or curvilinear manner to changing habitat variables. All analyses were performed using the R language and environment for statistical computing (R Core Team 2016).

Results

In total we sampled 2,240 sample units and collected a total of 9,733 larvae and juveniles (mean catch per unit effort [CPUE] 4.35) comprised of 14 different genera. There were 320 sample

units from our control stream where we collected 2,667 larvae and juveniles (mean CPUE 8.33), which were comprised of 11 genera. Our samples from dammed streams (1,920 sample units) resulted in the capture of 7,066 larvae and juveniles (mean CPUE 3.68) comprised of 14 genera. At dammed sites (960 sample units) with epilimnetic releases 4,200 larvae and juveniles were captured (mean CPUE 4.38) and 13 genera; while those with hypolimnetic releases (960 sample units) resulted in the capture of 2,866 larvae and juveniles (mean CPUE 2.99) and 10 genera.

Drainage area was unrelated to genera richness ($R^2=0.05$; $p>0.05$) for the streams we surveyed. There were significant changes along the longitudinal gradient (distance from dam) for abundance, richness, and diversity. Abundance and diversity differed between years (ANCOVA: $F=9.1$, $p<0.05$, $df=1$ and $F=5.9$, $p<0.05$, $df=1$ respectively) while richness did not (ANCOVA: $F=0.01$, $p>0.05$, $df=1$). Within year, differences existed between dam release type and control stream for abundance, richness, and diversity (ANCOVA: $F=16.31$, $p<0.05$, $df=2$; $F=116.9$, $p<0.05$, $df=2$; $F=78.9$, $p<0.05$, $df=2$ respectively). Post hoc tests revealed significant differences for richness and diversity for each pairwise comparison ($p<0.05$); however, for abundance differences between our control stream and each of the release types were significant ($p<0.05$) but differences between release types was not ($p>0.05$) (Figure 3).

Within dammed streams the difference between epilimnetic and hypolimnetic releases regarding mean absolute values of richness and diversity was most pronounced at moderate distances from dams (Figure 3). The greatest absolute difference was at 2100 m from dams for both richness and diversity. Additionally, there is an apparent very small difference between release types at sites near dams and in fact the absolute difference was smallest at distances between 100-400 m and 200-400 m below dams for richness and diversity respectively. However, when making comparisons as a percent difference, the smallest differences were more

variable in their location downstream from dams. For richness the three distances from dams (i.e., sites) with the greatest percent difference between release types were at 400 m, 1,600 m, and 5,100 m (6.5%, 13.3%, and 15.4% respectively) and for diversity the greatest percent differences between release sites were at 5,100 m, 3,100 m, and 400 m (5.7%, 6.2%, and 7.2% respectively). Whereas richness and diversity were consistently higher in streams with epilimnetic dam releases than hypolimnetic dam releases, this was not the case for abundance. Differences in abundance between the two release types were more variable along the stream continuum and at distances between 100-2100 m dams with hypolimnetic releases had higher abundances than those with epilimnetic releases.

Community structure—Differences existed in community structure between epilimnetic and hypolimnetic releases and control stream (Adonis: $F=8.12$, $p<0.05$, $df=1$). We therefore performed Non-metric multidimensional scaling (NMDS) analysis on the epilimnetic and the hypolimnetic data separately (Figure 4a, c, and e and b, d, and f respectively), where select variables are presented. For the purpose of displaying a comparison of each release type to the control stream we performed separate NMDS analyses on the epilimnetic and hypolimnetic data with our control stream (Figure 4a and b). Since our major goal was to understand the differences between epilimnetic and hypolimnetic community structure associations with habitat variables additional NMDS analyses were performed without including the control stream (Figure 4c-f).

Nonmetric multidimensional scaling indicated streams with epilimnetic dam releases were strongly structured by land cover variables and exhibited gradients associated with taxa richness and distance from dam (Figure 4a). When moving from right to left in Figure 4a both

distance and richness increased and epilimnetic community structure became increasingly similar to the control stream as evidenced by the large amount of overlap. Along with low richness, sites close to dams (right side of Figure 4a) were strongly characterized by higher values of the disturbed land cover (road density, % development, and % grassland; Only road density (Rd_dens) is shown.), and high conductivity. Sites with high richness (i.e., the left side of axis 1) were associated with higher % forest and cobble substrates and were more distant from dams (Figure 4c).

Fish communities in streams with epilimnetic releases were most strongly structured by a disturbance gradient followed by a water quality gradient. Most genera were negatively related to high levels of disturbance and positively associated with increased distance and higher richness. *Semotilus*, *Pimephales*, and *Notropis* loaded heavily on the left side of axis 1 and were therefore most associated with decreased disturbance (i.e., road density, % development, % grassland, and conductivity). Other taxa that showed a similar but not as strong of a relationship with the left side of axis 1 were *Rhinichthys*, *Nocomis*, and *Cottus* (only *Cottus* shown; Figure 4e). Along axis 2 for the epilimnetic data temperature loaded in the negative direction, while pH and dissolved oxygen were positively associated with the NMDS solution (Figure 4c). *Hypentelium*, *Ambloplites*, *Micropterus* and *Rhinichthys* were associated strongly with increasing temperature along axis 2. Of these four taxa, *Ambloplites*, *Hypentelium*, and *Micropterus* (only *Micropterus* shown; Figure 4c) were found in relatively high numbers in Yellow Creek, which had the highest average temperature (26.8 °C) of our sampled streams.

The NMDS for streams with hypolimnetic releases was unable to demonstrate that fish communities in these systems were structured by the measured habitat variables (in stream, land cover, and water quality) along the stream continuum below dams. Streams where water was

released hypolimnetically also showed a strong relationship with distance and richness along NMDS axis 1, but unlike in the epilimnetic ordination the linear model for distance performed poorly compared to that of the surface fit model (Table 1). The surface fit model (graphically not displayed) indicated a distance gradient from right to left along NMDS axis 1 and another from bottom to top along axis 2. As with streams with epilimnetic releases, those with hypolimnetic releases became more like the control stream as distance increased, but unlike the epilimnetic condition sites in streams with hypolimnetic releases showed little overlap with the control stream (New Creek) (Figure 4b). Habitat variables for the streams with hypolimnetic releases generally showed less variability than those with epilimnetic releases (Figure 4c vs 4d). Unlike streams with epilimnetic releases land cover had little importance in structuring communities in streams with hypolimnetic releases (Figure 4d). Along NMDS axis 1 in stream habitat (sandy substrate and boulders along the left side of the plot and gravel fines along the right side) and temperature (along the right side of the axis) were most influential in structuring these coldwater communities. Nonmetric multidimensional scaling axis 2 was most strongly influenced by cobble (top of the axis 2) and gravel fines and dissolved oxygen (bottom of axis 2) (Figure 4d). Hypolimnetic sites near dams indicated no strong association of larval and juvenile fish. Larval and juvenile fish became more strongly associated with sites that were mid-reach and those most distant from the dam as is indicated with *Semotilus* along NMDS axis 1 and *Percidae*, *Oncorhynchus*, and *Catostomus* along NMDS axis 2 (Figure 4f).

Non-metric multidimensional scaling showed that the community structure of larval and juvenile fish responded differently among epilimnetic, hypolimnetic, and control streams (Table 1). Distance was statistically correlated with the NMDS solution in epilimnetic, hypolimnetic, and control streams. Although correlations were relatively weak (r^2 values for linear

relationships ranged from 0.29 to 0.34), land cover variables were some of the strongest indicators (higher r^2 and significant p value) for both epilimnetic and control conditions but not for hypolimnetic streams, where only % grass covered area was significant ($r^2=0.06$; $p=0.04$). Of the channel morphology habitat variables boulder, fines, gravel fines, and sand were significantly correlated with streams with hypolimnetic releases but only boulder and sandy substrate were significantly correlated with epilimnetic streams and bedrock was the only substrate category significantly correlate with the control condition. In both epilimnetic and hypolimnetic conditions conductivity, dissolved oxygen, and temperature were significantly correlated and in the control condition significant correlations existed for conductivity and depth.

Surface fitting through the use of generalized additive models resulted in improved correlations with the NMDS solution and distance for impounded streams, but not our control stream. In streams with epilimnetic releases surface fits improved the r^2 for statistically significant variables over the linear models for % development, % forest, % grassland, road density, boulders substrate, sandy substrate, conductivity, pH, and temperature. Cobble substrate was not significant in the linear model but it was in the surface fit although the correlation was low ($r^2=0.07$; $p=0.02$). Only dissolved oxygen had a higher correlation coefficient in the linear model than the surface fit model; however, the values were very similar ($r^2=0.17$; $p<0.01$ and $r^2=0.16$; $p<0.01$ respectively). Streams with hypolimnetic releases responded somewhat differently in that the linear models outperformed the surface fit models for four out of five of the channel morphology variables (boulder substrate, fines, gravel fines, and sand), albeit improvements in r^2 were small. Surface fitting improved r^2 for % grassland, flow, conductivity, pH, dissolved oxygen, and temperature and in some cases, it did so substantially. For example, although the r^2 value was still low, the linear model for pH resulted in an $r^2=0.02$ ($p=0.47$) while

the r^2 for the surface fit model was 0.14 ($p < 0.01$). In our control stream all statistically significant habitat variables were improved with surface fitting over linear models and two variables (pH and dissolved oxygen) which were not significant with the linear models were significant with the surface fitting. Often, in our control stream, the surface fitting improved r^2 substantially (e.g., the linear model for dissolved oxygen resulted in $r^2 = 0.00$ ($p = 0.97$) while $r^2 = 0.26$ ($p = 0.03$) for the model with a surface fit.). Generally, land cover variables were important in streams with epilimnetic releases and our control stream where r^2 values were all > 0.30 and p-values were all < 0.01 . All water quality variables were important ($p \leq 0.03$) in both epilimnetic and hypolimnetic releases and our control stream (except temperature in the control stream) but r^2 were relatively low in impounded streams (i.e., ranging from 0.13 to 0.27) but had higher correlation in the control stream (i.e., ranging from 0.26 to 0.73). Additionally, the correlations for significant water quality variables within the control stream were higher (i.e., ranging from 0.26 to 0.73; Only temperature was non-significant [$p = 0.07$]) than those for impounded streams with epilimnetic or hypolimnetic releases (i.e., ranging from 0.07 to 0.39 for epilimnetic and 0.07 to 0.34 for hypolimnetic releases) where all p-values were < 0.01 .

Discussion

The results of our study suggest that differences may exist in community structure between streams with epilimnetic and hypolimnetic releases, as well as in the importance of land use and instream habitat factors that control community structure. Dam release type was influential on richness, diversity, and community structure. Lower temperatures (i.e., streams with hypolimnetic releases) generally resulted in lower values for richness and diversity. Generic richness and diversity were also influenced by land cover where disturbance at low levels increased values for both richness and diversity, corroborating the intermediate disturbance

hypothesis (Wilkinson 1999). Community structure of larval and juvenile fish in the dammed streams we sampled exhibited variability in their response to habitat variables depending on whether they were from streams with epilimnetic or hypolimnetic releases. While communities of both release types became more like the community of the control stream as distance from dams increased, those from epilimnetic releases showed more overlap with the control stream than the communities from streams with hypolimnetic releases. Based on our findings, communities in epilimnetic streams are likely to be more responsive to the habitat variables (i.e., land use and in stream) than are communities of hypolimnetic streams, which appear to respond most strongly to temperature.

Few studies have been performed in the context of the SDC on how fish are affected downstream of dams (Moog 1992; Parasiewicz *et al.* 1998). We found only one other study that systematically investigated the response of physicochemical and biological components of dams, which both dealt with aquatic macroinvertebrates as their biological component (Ellis and Jones 2013). We found no other studies that evaluated the effects of dams on larval and juvenile fish abundance, richness, diversity, and community structure that compared both epilimnetic and hypolimnetic releases to a control stream. Additionally, where typical studies have evaluated the SDC with sites spaced in a non-uniform manner across single or multiple streams, we systematically evaluated 16 sites per stream spaced equidistant along the stream continuum below each respective dam and at two spatial scales (the first seven sites were spaced 100-m apart and the remaining nine sites were spaced every 500-m to 5,100-m downstream of each respective dam). Ellis and Jones (2016) sampled four streams (two impounded and two natural flowing) at 6-8 non-equidistantly-spaced sites along each stream. Such a systematic approach allowed us to evaluate changes along the stream continuum in a consistent manner.

We investigated the longitudinal effect of dams, land use, and in stream habitat on downstream abundance, richness, and diversity of larval and juvenile fish. Additionally, we evaluated community structure and community/habitat associations using non-metric multidimensional scaling. Congruent with the theoretical construct of the SDC (Ward and Stanford 1983) in the dammed streams we sampled, the abundance, richness, and diversity of larval and juvenile fishes all generally increased with distance from the dam regardless of release type. In contrast, richness and diversity remained relatively consistent in our control stream and both were always greater than in dammed streams. Abundance was somewhat variable in our control stream and was sometimes greater and sometimes less than that of our dammed streams. While it is possible that our control stream was an outlier within the region (e.g., higher mean diversity than a “typical” undammed stream), our reason for including a control stream was to use it as a point of reference to compare dammed streams but not to statistically analyze differences between dammed and undammed streams. As such, dammed streams exhibited greater change across the sample distance than did New Creek (our control stream) in richness and diversity but not abundance.

Differences in richness and diversity between epilimnetic and hypolimnetic release types were evident, where streams with epilimnetic releases consistently had higher values. The streams we used in our study were each transitional, cool water systems (except Big Walnut Creek, OH, which was a warm water system) but waters released from the hypolimnion reduced water temperatures such that these streams were effectively cold water systems. It is likely that the reduced water temperature reduced the habitat suitability for the species that are available (i.e., transitional, cool water species) to colonize these cold water systems. Additionally, the small absolute differences between epilimnetic and hypolimnetic releases in richness and

diversity at sites near dams may be due to differences in the reproductive behavior of the species that perform well in cold water (i.e., hypolimnetic releases) versus epilimnetic releases. For example, trout migrate upstream into tributaries to spawn but when presented with a migration barrier (i.e., dam) they may spawn at sites close to the dam.

Other studies have focused on how dams affect downstream biota (Cortes *et al.* 2002; Rice *et al.* 2001) and habitat (Harvey 1987; Thompson *et al.* 2011). A review by Ellis and Jones (2013) covering studies published between 1980 and 2012 found 41 papers studying the biotic and abiotic impacts below dams. Of these, only three considered fish (Moog 1993; Gore *et al.* 1989; Parasiewicz *et al.* 1998). Physical habitat (substrate, often temperature) and food resources (aquatic and terrestrial invertebrates) are altered below dams which would be expected to have consequences for spawning, recruitment, and presence of fishes. Many stream fishes are benthic spawners, so starvation of sediments caused by dams would affect spawning habitat. Our results corroborate these findings, that in dammed streams, substrate coarseness and cobble substrate were important in structuring fish communities at intermediate distances from dams. However, communities in streams with epilimnetic releases were not as strongly influenced by habitat variables (except temperature) in comparison to those with hypolimnetic releases. Dams also create a *cul-de-sac* effect for lotic fishes whereby source populations and connectivity must largely occur from downstream. Therefore, where larvae are displaced at sites near dams either by entering the drift or due to insufficient habitat (e.g., flow refugia) there is no recolonization of larvae from upstream reaches. Dams change the aquatic invertebrate communities as well (Ellis and Jones 2013) which changes the prey resources for many lotic fishes and their young. Despite these documented alterations below dams, and the importance of recruitment by early life stages of fish in supporting populations, we found only one study that examined the effects

of dams on larval fishes. Song *et al.* (2018) examined the larval distribution, growth, and feeding by four taxa of Chinese Carp below the Three Gorges Dam in the Yangtze River. In that study, larvae collected nearest the dam had later peak abundance, reduced feeding levels, and lower growth than those collected further downstream.

In addition to our findings that larval and juvenile fish communities are structured by dam release type, land use, and habitat, we also found, while we did not specifically aim to evaluate it, a pattern of two recovery gradients for larval and juvenile fish richness and diversity. A rapidly changing gradient within the first 600-m below dams and a second, more gradual recovery gradient, that extended beyond our 5,100-m sampling reach. Changes that occur below dams may occur rapidly (our near dam gradient), while others may require a much greater distance to reach recover (e.g., thermal recovery). Ellis and Jones (2016) suggested, and we agree, that future studies investigating the SDC should be designed to systematically evaluate variables of interest at various spatial and temporal scales.

Regulated rivers have been studied extensively and the successful management of these systems demands a full understanding of their impact on both abiotic and biotic components of the ecosystems they influence. Our study compared both epilimnetic and hypolimnetic dam releases to a control condition and our study is the first to investigate dam impacts on larval and juvenile fish in such a systematic manner. It is likely that differences in the response of early life stage fish to dam release type (i.e., epilimnetic and hypolimnetic) will require different management strategies and therefore a full understanding of the distinct drivers that structure aquatic communities within each release type is important.

Our study was largely descriptive and exploratory; however, our results, the findings of other researchers, the paucity of studies investigating dam impacts on early life stage fish, and

the apparent lack of extensive systematic sampling design (i.e., location of sample site locations downstream of dams) clearly suggest more studies are needed to investigate responses of larval and juvenile fish in the context of the SDC. The importance of successful reproduction for continued success of fisheries in riverine systems is obvious and we suggest that more effort should be made to understand how reproduction is impacted in impounded systems. Such studies should include structure to evaluate the two spatial gradients discussed here, as well as include temporally longitudinal aspects. Further understanding of land use practices and tributary influences, as well as the inclusion of various scales (spatiotemporal and biotic) should be included in studies and will aid in further understanding of the SDC and how to best manage impounded systems.

The numerous studies that have examined SDC and discontinuity distances in aquatic invertebrates and the few involving fish, point to alterations of fish communities downstream of dams (Moog 1992; Parasiewicz *et al.* 1998; Song *et al.* 2017; present study). This is important given how widespread dams of varying sizes are across North America. According to the US Army Corps of Engineers, there are an estimated 90,580 dams in the United States (> 1 m tall) of these 45,178 are considered large dams (≥ 8 m tall), (http://nid.usace.army.mil/cm_apex/f?p=838:5:0::NO). Canada has 800 large dams (>10 m) and numerous smaller ones (<https://www.canada.ca/en/environment-climate-change/services/water-overview/management/dams-diversions.html>). With so many dams, it may be difficult in some sites to tease out local impairments from upstream dam impacts. This is an important consideration given that biotic indices are widely used to assess water quality and biotic integrity in lotic sites (Karr *et al.* 1981; Angermier and Karr 1986). Often, regulatory agencies use these biotic indices to evaluate regulatory compliance or to assess impacts on aquatic systems. Jones

(2013) pointed out that knowledge of dam impacts should be considered in biomonitoring employing benthic invertebrates. The present study expands this caution to fish IBI's given the documented alteration of fish early life stage spatial patterns by dams. Information on the recovery distances below dams for given taxa may be important in modifying indices to better account for coincident effects of dams.

Acknowledgements

The authors would like to thank the anonymous "reviewers" for their insight and thoughtful comments and suggestions. Funding was provided by Dominion Power and laboratory facilities were provided by the Wildlife and Fisheries Program in the Division of Forestry and Natural Resources at West Virginia University. This work was supported by the USDA National Institute of Food and Agriculture, McIntire Stennis project [WVA00115; accession #102954], and the West Virginia Agricultural and Forestry Experiment Station.

499 **Literature Cited**

- 500 Allan, J. D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems.
501 Annual Review of Ecological and Evolutionary Systems 35:257-284.
- 502 Angermeier, P.L. and J.R. Karr. 1986. Applying an index of biotic integrity based on stream-fish
503 communities: considerations in sampling and interpretation. North American Journal of
504 Fisheries Management 6:418-429.
- 505 Allan, J. D. and Johnson, L. B. 1997. Catchment-scale analysis of aquatic ecosystems.
506 Freshwater Biology 37:107-111.
- 507 Auer, N. A. 1982. Identification of larval fishes of the Great Lakes basin, with emphasis on the
508 Lake Michigan drainage. University of Michigan, Special Publication 82-3, Ann Arbor.
- 509 Cortes, R., Ferreira, M., Oliveira, S., and Oliveira, D. 2002. Macroinvertebrate community
510 structure in a regulated river segment with different flow conditions. River Research and
511 Applications 18(4):367-382.
- 512 Ellis, L. E. and Jones, N. E. 2013. Longitudinal trends in regulated rivers: a review and synthesis
513 within the context of the serial discontinuity concept. Environmental Reviews 21(3):136-
514 148.
- 515 Ellis, L.E. and N.E. Jones. 2016. A test of the serial discontinuity concept: longitudinal trends of
516 benthic invertebrates in regulated and natural rivers of Northern Canada. River Research
517 and Applications 32(3):462-472.
- 518 Falke, J. A., Fausch, K. D., Bestgen, K. R., and Baily L. L. 2010. Spawning phenology and
519 habitat use in a Great Plains, USA, stream fish assemblage: an occupancy estimation
520 approach. Canadian Journal of Fisheries and Aquatic Sciences 67:1942-1956.

- 521 Fausch, K. D., Torgersen, C. E., Baxter, C. V., and Li, H. W. 2002. Landscapes to riverscapes:
522 bridging the gap between research and conservation of stream fishes. *BioScience*
523 52:483-498.
- 524 Fraley, J. J. 1978. Effects of elevated stream temperatures below a shallow reservoir on a cold-
525 water macroinvertebrate fauna. Pages 257–272 in J. V. Ward and J. A. Stanford, editors.
526 The ecology of regulated streams. Plenum Press, New York.
- 527 Freedman, J. A., Lorson, B. D., Taylor, R. B., Carline, R. F., and Stauffer, J. R., Jr. 2013. River
528 of the dammed: longitudinal changes in fish assemblages in response to dams.
529 *Hydrobiologia* 727(1):19–33.
- 530 Graf, W. L. 1999. Dam nation: A geographic census of American dams and their large-scale
531 hydrologic impacts. *Water Resources Research* 35(4):1305–1311.
- 532 Gore, J.A., Nestler, J.M., and Layzer, J.B. 1989. Instream flow predictions and management
533 options for biota affected by peaking-power hydroelectric operations. *Regulated Rivers:*
534 *Research and Management*, 3: 35–48. doi:10.1002/rrr.3450030106.
- 535 Greenwood, J. J. D., and Robinson, R. A. 2009. Principles of Sampling. Pages 11-86 in W. J.
536 Sutherland, editor. *Ecological Census Techniques*, 2nd edition. Cambridge University
537 Press, New York.
- 538 Guzy, J.C., E.A. Eskew, B.J. Halstead, and S.J. Price. 2018. Influence of damming on anuran
539 species richness in riparian areas: A test of the serial discontinuity concept. *Ecology and*
540 *Evolution* 2018;00:1-12. <https://doi.org/10.1002/ece3.3750>
- 541 Hanks, R. D. 2016. The Influence of Dams on Downstream Larval and Juvenile Fish and
542 Benthic Macroinvertebrate Community Structure and Associated Physicochemical

- 543 Variables. Ph.D. Dissertation. Department of Wildlife and Fisheries Science, West
544 Virginia University, Morgantown, WV.
- 545 Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by
546 flooding. *Transactions of the American Fisheries Society* 116:851-855.
- 547
- 548 Holland-Bartels, L. E., Littlejohn, S. K., and Huston, M. L. 1990. Guide to larval fishes of the
549 upper Mississippi River. U.S. Fish and Wildlife Service Publication, LaCrosse,
550 Wisconsin.
- 551 Johnson, L B., Richards, C., Host, G. E., and Arthur, J. W. 1997. Landscape influences on
552 water chemistry in Midwestern stream ecosystems. *Freshwater Biology* 37:193-208.
- 553 Jones, N. E. 2010. Incorporating lakes within the river discontinuum: longitudinal changes in
554 ecological characteristics in stream–lake networks. *Canadian Journal of Fisheries and*
555 *Aquatic Sciences* 67(12):2058–2058.
- 556 Jones, N.E. 2013. Spatial patterns of benthic invertebrates in regulated and natural rivers. *River*
557 *Research and Applications* 29(3):343-351.
- 558 Karr, J.R. 1981. Assessment of biotic integrity using fish communities. *Fisheries* 6(6):21-27.
- 559 Katano, I., Negishi, J., Minagawa, T., Doi, H., Kawaguchi, Y., and Kayaba, Y. 2009.
560 Longitudinal macroinvertebrate organization over contrasting discontinuities: effects of a
561 dam and a tributary. *Journal of the North American Benthological Society* 28(2):331-351.
- 562 Kelso W. E., Kaller, M. D., and Rutherford, A. 2013. Collection, processing, and identification
563 of fish eggs and larvae and zooplankton. Pages 363-413 in A. V. Zale, D. L. Parrish, and
564 T. M. Sutton, editors. *Fisheries techniques*, 3rd edition. The American Fisheries Society,
565 Bethesda, Maryland.

- 566 Lessard, J. L. and Hayes, D. B. 2003. Effects of water temperature on fish and
567 macroinvertebrate communities below small dams. *River Research and Applications*
568 19:721-732.
- 569 MacArthur, R. H. and Wilson, E. O. 1967. *The theory of island biogeography*. Princeton
570 University Press, Princeton, New Jersey.
- 571 Maynard, C M. and Lane, S. N. 2012. Reervoir compensation releases: impact on the
572 macroinvertebrate community of Derwent River, Northumberland, United Kingdom—a
573 longitudinal study. *River Research and Applications* 28:692-702.
- 574 McCune B. and Grace, J. B. 2002. *Analysis of ecological communities*. MjM Software Design,
575 Gleneden Beach, Oregon.
- 576 Merriam, E. R., Petty, J. T., Merovich, G. T., Jr, Fulton, J. B., and Strager, M. P. 2011. Additive
577 effects of mining and residential development on stream conditions in a central
578 Appalachian watershed. *Journal of the North American Benthological Society* 30(2):399–
579 418.
- 580 Moog, O. 1993. Quantification of daily peak hydropower effects on aquatic fauna and
581 management to minimize environmental impacts. *Regulated Rivers: Research and*
582 *Management* 8:5-14.
- 583 Moore, K. M. S. and Gregory, S. V. 1988. Summer habitat utilization and ecology of cutthroat
584 trout fry (*Salmo clarki*) in Cascade Mountain streams. *Canadian Journal of Aquatic*
585 *Sciences* 45:1921-1930.
- 586 Niles, J. M. 2004. Examination of experimentally engineered larval fish habitat in the Marmet
587 Pool, Kanawha River, West Virginia. M.Sc. thesis. Department of Wildlife and
588 Fisheries Science, West Virginia University, Morgantown, WV.

- 589 Niles, J. M. and K. J. Hartman. 2007. Comparison of three larval fish gears to sample shallow
590 water sites on a navigable river. *North American Journal of Fisheries Management*
591 27:1126-1138.
- 592 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G.
593 L., Solymos, P., Stevens, M. H. H., and Wagner, H. 2016. *Vegan: Community Ecology*
594 *Package*. R package version 2.3-3.
- 595 Olden, J. D. and Naiman, R. J. 2010. Incorporating thermal regimes into environmental flows
596 assessments: modifying dam operations to restore freshwater ecosystem integrity.
597 *Freshwater Biology* 55:86-107.
- 598 Parasiewicz, S., Schmutz, S., and Moog, O. 1998. The effect of managed hydropower peaking on
599 the physical habitat, benthos and fish fauna in the River Bregenzerach in Austria.
600 *Fisheries Management and Ecology* 5(5):403–417.
- 601 Perkin J. S., Troia, M. J., Shaw, D., Gerken, J. E., and Gido, K. B. 2016. Multiple watershed
602 alterations influence fish community structure in Great Plains prairie streams. *Ecology of*
603 *Freshwater Fish* 25(1):141–155.
- 604 Poff, N. L., and Hart, D. D. 2002. How Dams Vary and Why It Matters for the Emerging Science
605 of Dam Removal. *BioScience* 52(8):659-668.
- 606 Power, M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams:
607 importance of stream depth and prey size. Pages 333-351 in W. C. Kerfoot and A. Sih,
608 eds. *Predation: Direct and Indirect Impacts on Aquatic Communities*. University of
609 New England Press, Hanover, NH.

- 610 R Core Team (2012). R: A language and environment for statistical computing. R Foundation
611 for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL [http://www.R-](http://www.R-project.org/)
612 [project.org/](http://www.R-project.org/)
- 613 Rice, S. P., Greenwood, M. T., and Joyce, C. B. 2001. Tributaries, sediment sources, and the
614 longitudinal organisation of macroinvertebrate fauna along river systems. *Canadian*
615 *Journal of Fisheries and Aquatic Sciences* 58(4):824–840.
- 616 Roy, A. H., Rosemond, A. D., Paul, M. L. J., Leigh, D. S., and Wallace, J. B. 2003. Stream
617 macroinvertebrate response to catchment urbanisation (Georgia, U.S.A.). *Freshwater*
618 *Biology* 48(2):329-346.
- 619 Schade, C. B. and Bonar, S. A. 2005. Distribution and abundance of nonnative fishes in streams
620 of the western United States. *North American Journal of Fisheries Management*
621 25:1386-1394.
- 622 Schlosser, I. J. 1987. The role of predation in age and size related habitat use by stream fishes.
623 *Ecology* 68:651-659.
- 624 Schlosser, I. J. 1988. Predation risk and habitat use by two size classes of stream cyprinid:
625 experimental test of a hypothesis. *Oikos* 52:36-40.
- 626 Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41(10):704-712.
- 627 Schnieder, D.C. 2001. The rise of the concept of scale in ecology. *Bioscience*. 51(7):545-553.
- 628 Tennessee Valley Authority. 1978. Impact of reservoir releases on downstream water quality and
629 uses. Special executive report. Division of Environmental Planning, Tennessee Valley
630 Authority.

- 631 Olivero Sheldon, A., A. Barnett, and M. G. Anderson. 2015. A stream classification for the
632 Appalachian Region. The Nature Conservancy, Eastern Conservation Science, Eastern
633 Regional Office. Boston, MA.
- 634 Song, Y., F. Cheng, B.R. Murphy, and S. Xie. 2018. Downstream effects of the Three Gorges
635 Dam on larval dispersal, spatial distribution, and growth of the four major Chinese carps
636 call for reprioritizing conservation measures. *Canadian Journal of Fisheries and Aquatic*
637 *Sciences* 75(1):141-151.
- 638 Stanford, J.A. and J.V. Ward. 2001. Revisiting the serial discontinuity concept. *River Research*
639 *and Applications* 17:303-310.
- 640 Storey, A. W., Edward, D. H., Gazey, P. 1991. Recovery of aquatic macroinvertebrate
641 assemblages downstream of the Canning Dam, Western Australia. *Regulated Rivers:*
642 *Research and Management* 6:213-224.
- 643 Sutherland W. J. ed. 2006. *Ecological Census Techniques*. 2nd ed. Cambridge University
644 Press. New York.
- 645 Thompson, L.C., Cocherell, S. A., Chun, S. N., Cech, J. J., and Klimley, A. P. 2011.
646 Longitudinal movement of fish in response to a single-day low pulse. *Environmental*
647 *Biology of Fish* 90: 253–261.
- 648 Townsend, C. R. and Scarsbrook, M. R. 1997. The intermediate disturbance hypothesis,
649 refugia, and biodiversity in streams. *Limnology and Oceanography* 42(5):938-949.
- 650 Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The
651 river continuum concept. *Canadian Journal of Fisheries and Aquaculture Science*
652 37:130-137.

- 653 Wallus, R., Kay, L. K., Simon, T. P., and Yeager, B. L. 2008. Reproductive biology and early
654 life history of fishes in the Ohio River drainage: Series. CRC Press, 2008.
- 655 Ward, J.V. and Stanford, J.A. 1983. The serial discontinuity concept of lotic eco- systems. In
656 Dynamics of Lotic Ecosystems, Fontaine TD, Bartell SM (eds). Ann Arbor Scientific
657 Publishers: Ann Arbor, MI; 29–42.
- 658 Ward, J. V., Tockner, K., Uehlinger, U., and Malard, F. 2001. Understanding natural patterns
659 and processes in river corridors as the basis for effective river restoration. Regulated
660 Rivers: Research & Management 17(4 5):311–323.
- 661 Webb, P. W. 1975. In Hydrodynamics and energetics of fish propulsion, Fisheries Research
662 Board of Canada Bulletin 190.
- 663 Weins J.A. 1989. Spatial scaling in ecology. Functional Ecology. 3:385-397.
- 664 Werner, E. E. and Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size
665 structured populations. Annual Review of Ecological Systems 15:395-425.
- 666 Wilbur, H. M. 1980. Complex life cycles. Annual Review of Ecological Systems 11:67-93.
- 667 Wilkinson, D.M. 1999. The disturbing history of intermediate disturbance. Oikos 84(1):145-
668 147.
- 669 Wolf, A. E., Willis, D. W., and Power, G. J. 1996. Larval fish community in the Missouri River
670 below Garrison Dam, North Dakota. Journal of Freshwater Ecology 11(1):11-19.
- 671 Wood, S. 2006. Generalized additive models: an introduction with R. Chapman and Hall,
672 Boca Raton, Florida.
- 673 Yeager, B. L. 1993. Dams. Pages 57 – 113. In C. F. Bryan and D. A. Rutherford, editors.
674 Impacts on warmwater streams: Guidelines for evaluation, Second Edition. Southern
675 Division, American Fisheries Society, Little Rock, Arkansas.

676 Zurr, A. F., Leno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. 2009. Mixed effects
677 models and extensions in ecology with R. 1st edition. Springer, New York.

Draft

Table Captions

Table 1. Relationships of distance and habitat (land cover type, channel morphology, and water quality) to nonmetric multidimensional scaling (NMDS) ordination of larval and juvenile fish genera in 3 dimensions by vector fitting (linear model) and surface fitting (nonlinear generalized additive model). Corresponding r^2 and p-values are given. p-values are estimated from 1000 randomizations of the data. BL=boulder; BR=bedrock; CB=cobble; FN=finest; GC=coarse gravel; GF=fine gravel; SA=Sand; Cond=conductivity; DO=dissolved oxygen; Temp=temperature.

688 Table 1.

Variable	Epilimnetic		Hypolimnetic		Control	
	Vector r^2 (p -value)	Surface r^2 (p -value)	Vector r^2 (p -value)	Surface r^2 (p -value)	Vector r^2 (p -value)	Surface r^2 (p -value)
Distance	0.30 (<0.001)*	0.32 (<0.0001)*	0.08 (0.03)*	0.26 (<0.001)*	0.32 (<0.01)*	0.30 (<0.01)*
<i>Land cover</i>						
% Development	0.34 (<0.001)*	0.39 (<0.001)*	0.03 (0.31)	0.01 (0.29)	0.31 (<0.01)*	0.33 (<0.001)*
% Forest	0.29 (<0.001)*	0.35 (<0.001)*	0.01 (0.72)	0.03 (0.13)	0.32 (<0.01)*	0.34 (<0.01)*
% Grassland	0.29 (<0.001)*	0.35 (<0.001)*	0.06 (0.04)*	0.11 (<0.01)*	0.33 (<0.01)*	0.35 (<0.01)*
Road density	0.29 (<0.001)*	0.36 (<0.001)*	0.01 (0.84)	0.01 (0.26)	0.28 (<0.01)*	0.30 (<0.01)*
<i>Channel morphology</i>						
BL	0.07 (0.04)*	0.08 (0.02)*	0.09 (<0.02)*	0.08 (0.02)*	0.01 (0.83)	0.06 (0.25)
BR	0.02 (0.39)	0.00 (0.33)	0.03 (0.26)	0.01 (0.29)	0.19 (0.03)*	0.36 (<0.01)*
CB	0.06 (0.06)	0.07 (0.02)*	0.04 (0.17)	0.02 (0.18)	0.07 (0.35)	0.01 (0.33)
FN	0.03 (0.3)	0.02 (0.23)	0.08 (0.03)*	0.05 (0.03)*	0.01 (0.92)	0.00 (0.99)
GC	0.00 (0.91)	0.00 (0.90)	0.03 (0.24)	0.01 (0.24)	0.11 (0.21)	0.15 (0.12)
GF	0.02 (0.43)	0.06 (0.06)	0.34 (<0.001)*	0.33 (<0.001)*	0.09 (0.30)	0.06 (0.26)
SA	0.14 (<0.01)*	0.17 (<0.001)*	0.07 (0.04)*	0.05 (0.04)*	0.05 (0.44)	0.17 (0.10)
Coarse	0.03 (0.32)	0.03 (0.16)	0.05 (0.11)	0.03 (0.11)	0.12 (0.17)	0.10 (0.14)
Flow	0.03 (0.26)	0.02 (0.23)	0.05 (0.10)	0.17 (<0.01)*	0.01 (0.91)	0.00 (0.79)
Depth	0.04 (0.16)	0.11 (<0.01)	0.05 (0.12)	0.02 (0.12)	0.31 (<0.01)*	0.47 (<0.001)*
<i>Water quality</i>						
Cond	0.11 (<0.01)*	0.19 (<0.001)*	0.10 (<0.01)*	0.13 (<0.01)*	0.63 (<0.001)*	0.73 (<0.001)*
pH	0.12 (<0.01)*	0.21 (<0.001)*	0.02 (0.47)	0.14 (<0.01)*	0.14 (0.11)	0.34 (<0.01)*
DO	0.17 (<0.001)*	0.16 (<0.001)*	0.16 (<0.01)*	0.27 (<0.001)*	0.00 (0.97)	0.26 (0.03)*
Temp	0.23 (<0.001)*	0.24 (<0.001)*	0.10 (<0.01)*	0.14 (<0.01)*	0.13 (0.15)	0.17 (0.07)

689

Figure Captions

Figure 1. A) Inset of the eastern United States showing the study region. B) Location of study streams and dams. Dammed streams with hypolimnetic releases are designated by solid squares, while solid circles represent dammed streams with epilimnetic releases. OH-Ohio; PA-Pennsylvania; MD-Maryland; WV-West Virginia. C) Displays the spacing of sample sites along the stream continuum below dams using Beaver Run as an example. Data for the map were obtained from the National Hydrography Dataset Plus v2 and the National Inventory of Dams.

Figure 2. Schematic of (a) the 16 sampling sites along the stream continuum below a dam and (b) an individual sample site within a stream. Larval fish were sampled for a total of 25 minutes within each sample site (five, five-minute periods). Dissolved oxygen, conductivity, temperature, and pH were recorded at once at each sample site per visit. Channel and bankfull widths were measured at each transect per visit. Habitat measurements (width, depth, flow, percent embedment, and substrate were measured) were recorded for at five point locations (solid circles) along each of the five transects at a sample site per visit.

Figure 3. Richness, abundance, and diversity for epilimnetic, hypolimnetic, and control conditions. Approximate 95% pointwise confidence intervals are given by shaded regions. Three streams were sampled for both epilimnetic and hypolimnetic release types and a single stream (un-dammed stream) was treated as a control stream.

711 Figure 4. Nonmetric multidimensional scaling (NMDS) ordination of larval and juvenile fish
712 samples (Bray-Curtis coefficient) in 2 dimensions labeled by release type (epilimnetic,
713 hypolimnetic, and control condition as denoted by squares, triangles, and circles respectively) (a
714 and b), habitat variables (instream, land cover, and water quality) (c and d), and weighted mean
715 position of genera of larval and juvenile fish. In a and b the size of the respective shape is
716 representative of average site level taxonomic richness. Stress = 11.0 and 8.7 for epilimnetic (c
717 and e) and hypolimnetic (d and f) dam releases respectively in the 3-dimensional solution. Two
718 convergent solutions were found after one and 20 runs for epilimnetic and hypolimnetic dam
719 releases respectively. DO = dissolved oxygen, Cond = conductivity, Temp = temperature, Dist =
720 distance, Pgrass = % grassland, Pdev = % development, Pfor = % forested land, Rd_dens = Road
721 density, Coarse = substrate coarseness, BL = boulder, BR = bedrock, CB = cobble, GC = coarse
722 gravel, GF = fine gravel, SA = sandy substrate, SEM = *Semotilus*, COT = *Cottus*, PIM =
723 *Pimephales*, CAMP = *Campostoma*, NOC = *Nocomis*, ETH = *Etheostoma*, PERC = *Percina*,
724 NOTR = *Notropis*, RHY = *Rhinichthys*, HYP = *Hypentelium*, AMBL = *Ambloplites*, MICR =
725 *Micropterus*, CAT = *Catostomus* and ONC = *Oncorhynchus*. Vectors show linear trends where
726 the length of a vector for a specified variable is indicative of the relative correlation strength
727 (scaled to unit length) where its direction indicates the direction of most rapid increase in
728 ordination space.

Figure 1

Figure 2.

Figure 3.

Figure 4