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ARTICLE

Isolating causal pathways between flow and fish in the regulated river hierarchy

Ryan A. McManamay, Brandon K. Peoples, Donald J. Orth, Charles A. Dolloff, and David C. Matthews

Abstract: Unregulated river systems are organized in a hierarchy in which large-scale factors (i.e., landscape and segment scales) influence local habitats (i.e., reach, meso-, and microhabitat scales), and both differentially exert selective pressures on biota. Dams, however, create discontinua in these processes and change the hierarchical structure. We examined the relative roles of hydrology and other instream factors, within a hierarchical landscape context, in organizing fish communities in regulated and unregulated tributaries to the Upper Tennessee River, USA. We used multivariate regression trees to identify factors that partition fish assemblages based on trait similarities, irrespective of spatial scale. We then used classical path analysis and structural equation modeling to evaluate the most plausible hierarchical causal structure of specific trait-based community components, given the data. Both statistical approaches suggested that river regulation affects stream fishes through a variety of reach-scale variables, not always through hydrology itself. Although we observed different changes in flow, temperature, and biotic responses according to regulation types, the most predominant path in which dam regulation affected biota was via temperature alterations. Diversion dams had the strongest effects on fish assemblages. Diversion dams reduced flow magnitudes, leading to declines in fish richness but increased temperatures, leading to lower abundances in equilibrium species and nest guarders. Peaking and run-of-river dams increased flow variability, leading to lower abundances in nest-guarding fishes. Flow displayed direct relationships with biotic responses; however, results indicated that changes in temperature and substrate had equal, if not stronger, effects on fish assemblage composition. The strength and nature of relationships depended on whether flow metrics were standardized for river size. We suggest that restoration efforts in regulated rivers focus on improving flow conditions in conjunction with temperature and substrate restoration.

Résumé : Les réseaux fluviaux non régularisés sont organisés selon une hiérarchie dans laquelle des facteurs à grande échelle (c.-à-d. à l'échelle du paysage et du segment) influencent les habitats locaux (c.-à-d. à l'échelle du tronçon et des méso- et microhabitats), ces deux types de facteurs exerçant des pressions de sélection différentes sur le biote. Les barrages créent toutefois des discontinuités dans ces processus et modifient la structure hiérarchique. Nous avons examiné les rôles relatifs de l'hydrologie et d'autres facteurs du cours d'eau, dans un contexte de paysage hiérarchique, dans l'organisation des communautés de poissons dans des affluents régularisés et non régularisés de la rivière Upper Tennessee (États-Unis). Nous avons utilisé des arbres de régression multivariée pour cerner les facteurs qui divisent les assemblages de poissons selon des similitudes de caractères, quelle que soit l'échelle spatiale. Nous avons ensuite utilisé l'analyse de dépendance classique et la modélisation d'équations structurales pour évaluer la structure causale hiérarchique la plus plausible de composantes de la communauté basées sur des caractères précis, étant donné les données. Les deux approches statistiques indiqueraient que la régularisation des rivières influence les poissons des cours d'eau par l'entremise de diverses variables à l'échelle du tronçon, mais pas toujours par l'entremise de l'hydrologie comme telle. Bien que nous ayons observé différentes modifications du débit, de la température et des réactions biotiques selon le type de régularisation, la voie causale dominante par laquelle la régularisation par un barrage influençait le biote est la modification des températures. Les barrages de dérivation exerçaient les effets les plus forts sur les assemblages de poissons, en réduisant la magnitude des débits, menant du coup à la diminution de la richesse des poissons, mais ils causaient une augmentation des températures, entraînant une diminution de l'abondance chez les espèces en équilibre et les gardeurs des nids. Les barrages de pointe et au fil de l'eau accroissaient la variabilité des débits, menant à de plus faibles abondances des poissons gardeurs de nid. Si le débit présentait des relations directes avec les réactions biotiques, les résultats indiquent toutefois que les modifications de la température et du substrat avaient des effets égaux, voire plus grands sur la composition des assemblages de poissons. La force et la nature des relations dépendent de la normalisation ou non des paramètres d'écoulement en fonction de la taille de la rivière. Nous suggérons que les efforts de restauration dans les rivières régularisées devraient s'axer sur l'amélioration des conditions d'écoulement, combinée au rétablissement de la température et à la restauration du substrat. [Traduit par la Rédaction]

Introduction

River systems are a continuous matrix of lateral, longitudinal, and vertical processes that shape the habitats in which fishes complete their life cycles (Fausch et al. 2002). Conceptualizing river habitats as the outcome of cumulative and interacting processes influences how scientists and managers view species conservation, community ecology, and river restoration (Ward et al. 2001). Of the many drivers of river organization, streamflow regimes operate at multiple spatial and temporal scales and control many of the interacting processes that structure ecological com-

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R.A. McManamay. Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008 MS6351, Oak Ridge, TN 37831-6351, USA.
B.K. Peoples and D.J. Orth. Department of Fish and Wildlife Conservation, Virginia Tech, 100 Cheatham Hall, Blacksburg, VA 24061, USA.
C.A. Dolloff. USDA Forest Service, Department of Fish and Wildlife Conservation, Virginia Tech, 350 Latham Hall, Blacksburg, VA 24061, USA.
D.C. Matthews. Tennessee Valley Authority, 400 West Summit Hill Drive, Knoxville, TN 37902, USA.
Corresponding author: Ryan A. McManamay (e-mail: mcmanamayra@ornl.gov).

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munities in unregulated river ecosystems (Poff et al. 1997). In fact, the natural flow regime has been termed the "master variable" that shapes the physiochemical template that riverine organisms need to survive (Power et al. 1995).

Linkages among flow regimes, physiochemical habitats, and fishes are apparent in natural free-flowing river systems (Kirsch and Peterson 2014), but dams can either remove or change the nature of these relationships (Mims and Olden 2013). Dams simultaneously alter multiple components of river systems, effectively disconnecting flow and other physiochemical processes, such as sediment transport (Kondolf 1997; Trush et al. 2000) and thermal regimes (Caissie 2006; Olden and Naiman 2010); alterations of either of these components lead to habitat degradation and loss for fishes (Gordon et al. 2004). Despite this knowledge, most restoration efforts downstream of dams in the United States (with the exception of dam removal and salmonid recovery efforts) focus primarily on reinstating natural flow conditions (Bernhardt et al. 2005; Sudduth et al. 2007), without improving sediment transport (Jackson and Pringle 2010), temperature regimes (Olden and Naiman 2010), or habitat complexity (Roni et al. 2015). This emphasis on flow enhancement likely stems from the perception in the scientific literature that improving hydrologic conditions best approximates "process-driven" restoration, since reestablishing processes (as opposed to habitat enhancements) instates self-regulating mechanisms of river habitat formation and maintenance (Roni et al. 2008). For example, when considering disturbances from dams, ecological alteration is commonly assumed a direct result of hydrologic alteration as opposed to temperature alteration or fragmentation (Poff and Zimmerman 2010; Carlisle et al. 2011; Taylor et al. 2014).

It is widely acknowledged that river systems are hierarchical, where elements at larger scales (e.g., basins, segments) operate simultaneously and unidirectionally to influence structural elements at smaller scales (e.g., reaches, meso- and microhabitats) (Petts 1984; Frissell et al. 1986) and ultimately aquatic life (Kirsch and Peterson 2014). The structural organization of variables creates a complex web of environmental drivers that determine the biotic composition of rivers (Jackson et al. 2001). Thus, the overarching goal of this study is to understand where flow (measured at the reach scale) sits within this hierarchy. Doing so will contribute to a proper understanding of the hierarchical processes that govern stream ecosystem structure and ensure effective management and restoration of regulated river systems (Roni et al. 2008). Restoring aspects of the natural flow regime in regulated river systems has proven effective in the recovery of biological communities in some systems (Travnichek et al. 1995; Propst and Gido 2004; Lamouroux et al. 2006) but not in others (Krause et al. 2005; McManamay et al. 2013). Flow restoration alone may be inadequate (Bednarek and Hart 2005) or may even cause species loss if not accompanied by the restoration of other aspects of river ecosystems (Jackson and Pringle 2010). Typically, water allocation or reregulation decisions require specific and accurate predictions at a given location (Harvey et al. 2014), which require highly quantitative and structural models to tease apart the importance of flow versus other factors and ensure river management is relevant (Webb et al. 2015).

Landscape-scale patterns, such as habitat connectivity or fragmentation, and their relation to reach-scale processes ultimately determine the ability of many species to persist in river segments (Fausch et al. 2002; Reid et al. 2008), while local habitat variables influence the presence of fishes within reaches. Herein, we examine the relative role of hydrology in structuring instream habitats and fish communities in rivers of the Upper Tennessee River Basin, USA, experiencing different types of dam regulation (including unregulated streams). We used two modeling techniques (multivariate regression trees and structural equation modeling) with predictor variables summarized at the basin or segment levels (i.e., large scale) and the instream habitat level. We first sought to identify factors structuring fish assemblages on the basis of species traits (life history strategies and reproductive groups), irrespective of spatial hierarchy. We then sought to evaluate the hierarchical structure of large-scale and local factors that affect specific components of fish assemblages, emphasizing particularly the relative role of hydrology in this hierarchy. We hypothesized that large-scale factors, such as dam regulation, interbasin variability, and valley segment gradient, operate indirectly through instream habitat factors (e.g., flow, temperature, substrate) to influence fish assemblages. We compared hypothetical hierarchical structures indicating that flow influences assemblage components directly, through other instream habitat factors, or not at all.

Study sites

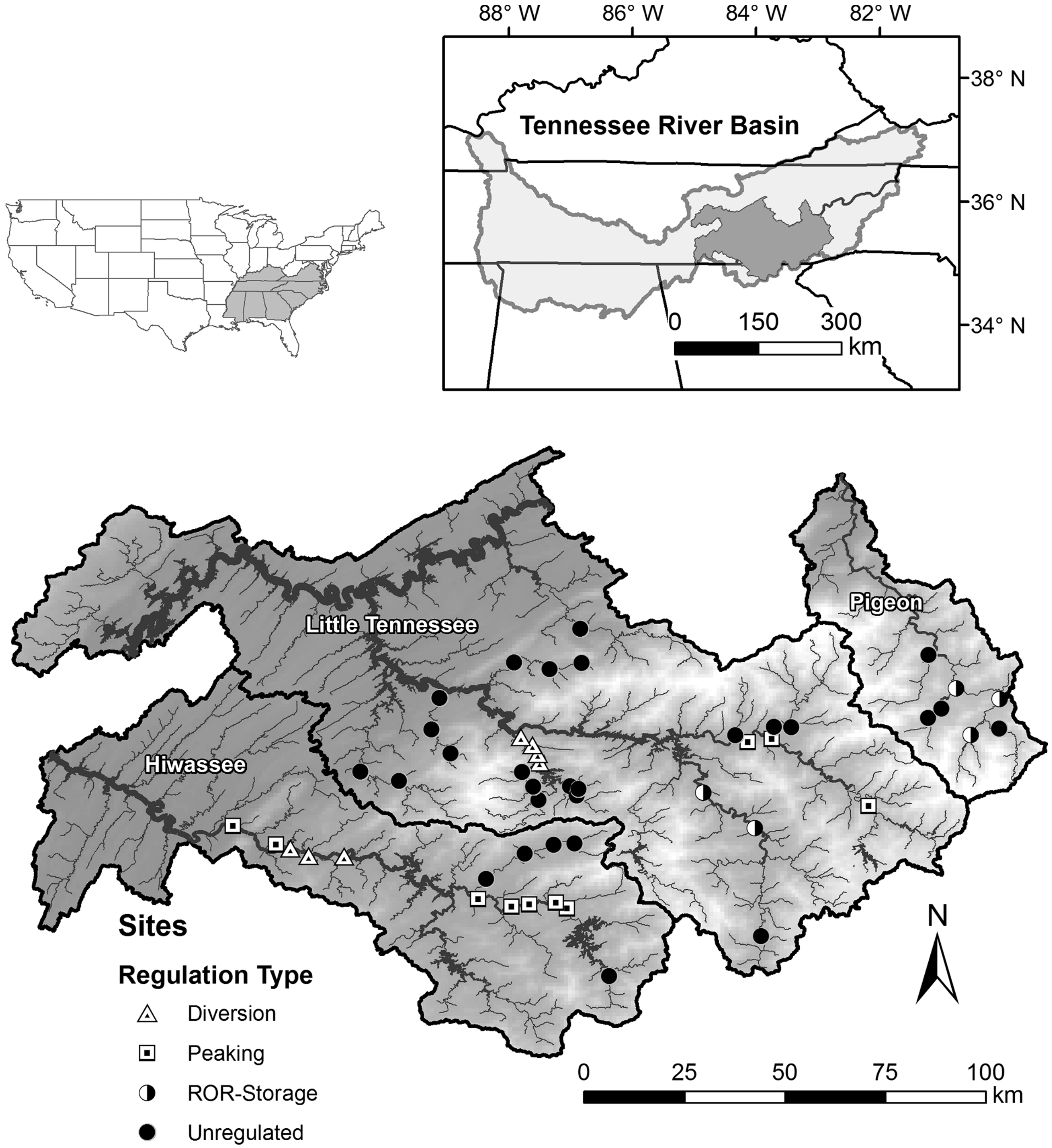
Fish assemblage sampling sites (n = 50) were located within the Little Tennessee River, Hiwassee River, and Pigeon River drainages in the Blue Ridge Physiographic Province (Fig. 1) (McManamay et al. 2013). Sites consisted of stream reaches demarcated on the up- and downstream ends as five to six times the bankfull width. Measurements of environmental predictors of fish community dynamics were made at a larger scale (watershed or segment levels) or within these reaches (instream habitat) (methods provided below). Twenty-eight of the sites were located in streams of unregulated flow (above dams), whereas the remaining 22 sites were located in streams whose flows were regulated by dams. Sites were typically larger systems (mean drainage area = 595 km^2) and were selected within valleys with lower gradients (0.09% to 2.4%, mean = 0.6%) to compare fish assemblage characteristics in regulated rivers with those in unregulated rivers. Additional site descriptions are provided in McManamay et al. (2013).

Methods

Overview

Conclusions regarding the role of environmental variables, such as flow, in predicting ecological dynamics can be influenced by the statistical approach taken, among other factors. To avoid potential biases, we employed two modeling approaches, one being an exploratory technique without any a priori hypothesized structure, and the other being completely dependent upon hypothesized structural relationships (Fig. 2). Using multivariate regression tree (MRT) analysis as an exploratory analysis, we first sought to identify factors that partition fish community types on the basis of similarities in proportional representation of life history groups (Winemiller and Rose 1992) and reproductive groups (Balon 1975), irrespective of hierarchical spatial structure. We then used path analysis coupled with structural equation modeling (SEM) to identify causal pathways through which a hierarchically arranged suite of factors operate to influence specific components of fish assemblages. We conceptualized a hierarchical structure in which most large-scale factors influence biota indirectly by affecting instream habitat, which affects biota directly. We organized predictors of fish assemblage structure at two hierarchical scales: (1) large scale and (2) instream habitat scale (Table 1). Large-scale factors were measured at the valley segment, watershed, or even basin (eight-digit hydrologic unit code, HUC) levels. Instream habitat variables, including flow regimes, were measured at the reach scale. Although hydrology can operate at scales larger than reaches, tributary inflow and hydrologic modification from dams can create localized conditions that vary considerably from reach to reach and with distance from dam. However, hydrology, different from other instream habitat variables, was allowed to exert hierarchical controls on other instream habitat variables (Fig. 2). In doing so, we were able to evaluate hypotheses specifying that (*i*) both flow and other instream habitat variables influence fish assemblage components directly, (*ii*) flow influences assemblage components indirectly by affecting other instream habitat variables that directly affect bi-

Fig. 1. Unregulated and regulated sites used in the current study. Major basins within the Tennessee River system are labeled. ROR, run-of-river.



ota, (*iii*) flow is the only instream factor affecting fishes, or (*iv*) flow plays a diminished role in affecting fish assemblage components, relative to other factors (e.g., temperature, substrate, channel morphology). Explanatory variables are listed in Table 1. Many of the variables were previously compiled by McManamay et al. (2013); thus we only elaborate on undocumented methods below.

Large-scale factors

Using information from the National Dam Inventory database (USACE 2013), internet sources, and field reconnaissance visits, we first classified regulated sites into three groups of similar dam operations on the basis of flow regulation at the nearest upstream dam. Distance to upstream dams averaged (±SE) 16 (±3.4) km and ranged from 0.6 to 60 km. Peaking dams store and release water in pulses to generate electricity, causing rapid hydrologic fluctuations. In contrast, storage and run-of-river (ROR) dams are smaller and release flows in approximation with inflows and typically have less influence on hydrology. Diversion projects divert water around a stream channel for downstream power production. Sites classified as diversions were located within bypass channels, i.e., stream reaches in which water is diverted around. All sites not regulated by dams were classified as "unregulated". To consider large-scale exogenous controls, such as interbasin differences in habitat structure, we classified all sites according to their location in one of the three major basins: the Hiwassee, Little Tennessee, and Pigeon rivers (Fig. 1); see "Statistical analyses" section below for how these factors were included in MRTs and SEMs.

We used 30 m digital-elevation models to delineate watersheds and calculate watershed areas (km²) for each site. River

Fig. 2. Four generalized hypothetical hierarchical structures depicting the relative roles of large-scale and instream factors (see Table 1) on components of stream fish assemblages (proportions of life history and reproductive groups, and species richness) in regulated and unregulated tributaries to the Upper Tennessee River, USA. Hypotheses specified that (A) both flow and other instream habitat variables influence fish assemblage components directly, (B) flow influences assemblage components indirectly by affecting other instream habitat variables which directly affect biota, (C) flow is the only instream factor affecting fishes, or (D) flow plays a diminished role in affecting fish assemblage components, relative to other factors. All hypotheses specify that fragment length affects fishes directly by limiting dispersal. For clarity, arrows beginning or terminating at a dashed box indicate influence from or to all variables within the box. Conversely, arrows to or from a specific variable(s) within a dashed box indicate hypothesized relationships specific to the variable(s).

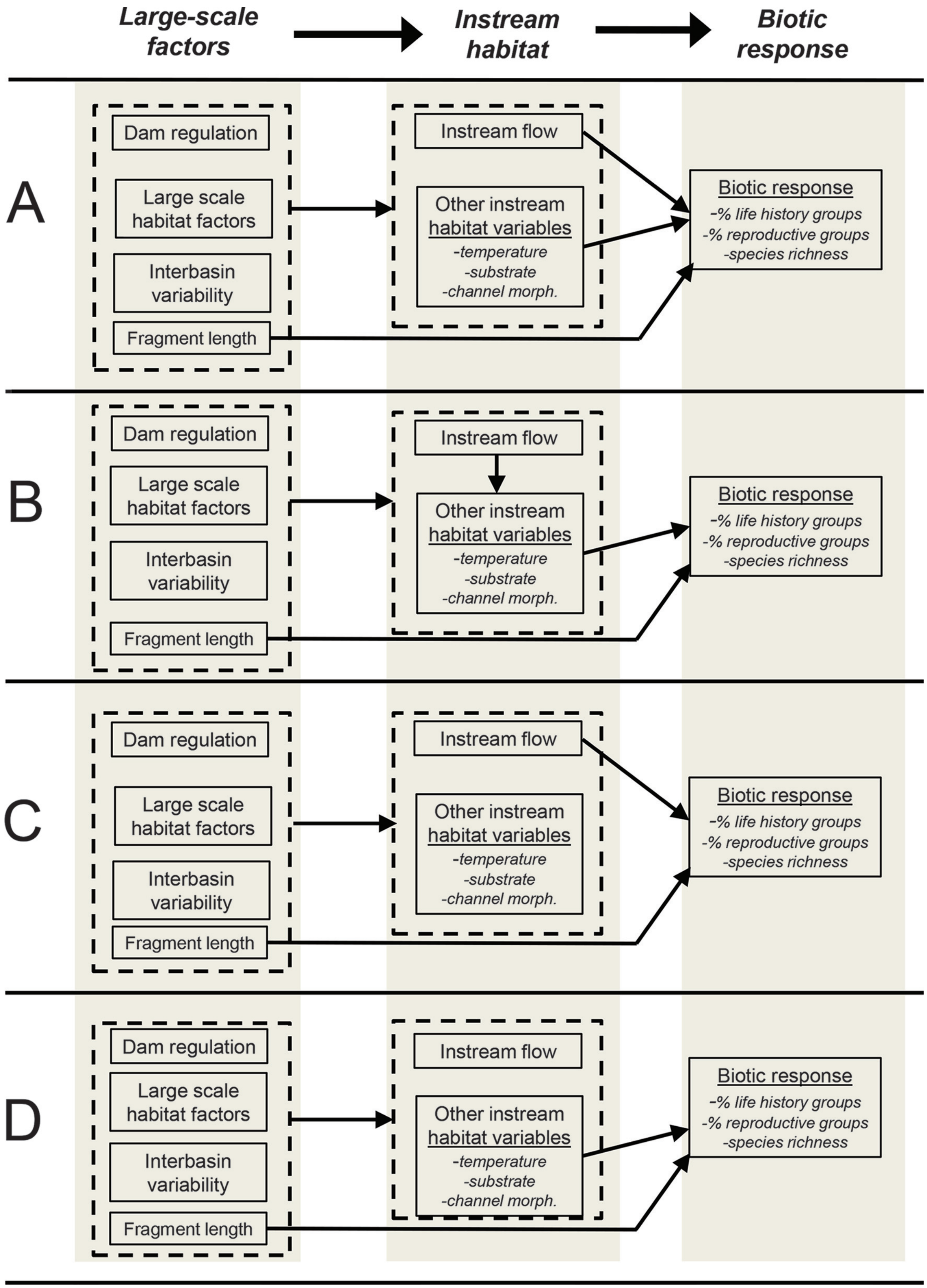


Table 1. Explanatory variables used in the analyses.

Variable	Description
Large-scale factors	
Hydrologic basins	
HUC-1	Pigeon River
HUC-2	Hiwassee River
HUC-3	Little Tennessee River
Watershed predictors	
DA_SQKM	Drainage area (km^2)
Elevation	Elevation (m)
Gradient	Gradient (proportion rise/run) measured over distance of seven times bankfull width
DEV	% Developed land in upstream watershed
AGR	% Agriculture land in upstream watershed
Dam regulation	
DIV	Diversion (surface release)
ROR-S	Run-of-river or water supply
Peak	Peaking (bottom release)
UR	Unregulated
Instream factors	
Flow*	
MA3	Daily CV
MA2†	Mean annual flow
ML17	Baseflow index (1-day low flow divided by mean daily flow)
FL1	Low-flow frequency
FH6	High-flow frequency
DL1‡	1-day minimum flow
DL5‡	90-day minimum flow
Channel morphology	
BFW	Bankfull width (m)
ENTR	Entrenchment ratio (width of floodplain at two times bankfull width/bankfull width)
Bar_Hab	Bar habitat index (areal coverage bars divided by the total area surveyed within the reach)
Substrate*	
D_{25}	25% Percentile substrate size
D_{50}	Median substrate size
D_{75}	75% Percentile substrate size
% Sand	% of substrate (<2 mm)
% Gravel	% of substrate (>2 mm and <64 mm)
% Cobble	% of substrate (>64 mm and <256 mm)
% Boulder	% of substrate (>256 mm and <2046 mm)
% Bedrock	% of substrate (>2046 mm)
Subsurface	% of armored substrate with sand or gravel underneath

*Indicates variables were used in principal components analysis.
†MA2 was divided by drainage area in scaled flow scenario.
‡Indicates variables were divided by MA2 in scaled flow scenario.

fragmentation was calculated as the sum of the free-flowing distance from each site to the nearest upstream dam and downstream to the nearest dam. In the case of unregulated rivers, fragmentation was measured as the sum of the distance upstream to the headwaters of the largest tributary downstream to the nearest dam. Valley slope was measured as proportional change in elevation over a 1 and 2 km distance and validated using field-based measurements of slope taken with level and stadia rod (Harrelson et al. 1994). Percentages of agriculture (pasture, hay, cultivated crops) and developed land (low, medium, and high intensity) within each site's watershed were calculated using the 2006 National Land Cover Dataset (MRLC 2014).

Instream habitat factors

Morphology

Each site was visited once to quantify channel morphology and substrate conditions during the latest year of fish sampling (see fish sampling section). We focused instream habitat measurements on riffle and riffle–run habitats because they are indicative of larger-scale dynamics such as dam regulation. For example, riffles are areas of active sediment transport (Gordon et al. 2004) and represent a river's regular transport potential (Kappesser 2002); thus riffles are most likely to respond to dam regulation (e.g., degradation, armoring). We assume that pool and run habitats show less consistent responses to dam regulation; hence non-riffle-dwellers are more likely to respond to dam regulation through other pathways besides substrate (e.g., flow and pool depth).

We measured instream habitat at four cross-sectional transects per site according to Jowett (1993). In smaller streams, we established transects in the center of four separate riffles; however, in larger streams (>60 m wide), we isolated at least two different riffles and established two transects at equal distances from the center of each (some riffles in larger streams exceeded 200 m in length). Along each transect, we established benchmarks for measuring bankfull width according to Harrelson et al. (1994). We measured the entrenchment ratio as the width of the floodplain measured at two times the bankfull height divided by the bankfull width. High entrenchment ratios indicate higher connectivity between a river channel and its floodplain. Bar habitat index was estimated as the total areal coverage of point, lateral-alternating, and mid-channel bars (of various size material) and dividing that value by the total area surveyed within the reach.

Substrate

Along each transect, we measured substrate sizes for ≥100 particles using a Wolman pebble count and categorized substrates on the basis of a simplified Wentworth scale (e.g., sand: <2 mm, gravel: 2–64 mm, etc.). We characterized substrate sizes as D_{25} (particle size of 25th percentile), D_{50}, and D_{75}, and substrate size diversity as percentages of particles falling into each size category. To quantify substrate embeddedness, we calculated a subsurface index by randomly choosing a cobble or boulder, lifting it from the streambed, and determining whether there was sand or fine gravel underneath (2–4 mm) at 10 equidistant points on each transect.

Temperature

Temperature values were collected at the site reach within the last 15 years and represented averages from mid-June to mid-September. We collected temperature data (*i*) directly via temperature loggers (10 sites), (*ii*) from the US Geological Survey (USGS) National Water Information System (26 sites), or (*iii*) as continuous or intermittent (point sampling) temperature data or reports from regional biologists (14 sites). Most data from biologists were continuous or were reported averages from continuous sampling. Point samples were screened to have at least five samples per month to provide adequate averages. Average temperatures represent variation among sites, including the influence of dam regulation, as opposed to capturing year-to-year variation at each site.

Flow

Daily discharge records for each site were previously compiled by McManamay et al. (2013) using a combination of USGS stream gauge records, spillage from dams, and modeling techniques. The flow metrics we used summarize patterns across at least a 20-year period and do not represent within-year variability. Using daily discharge records, hydrologic statistics were calculated for each hydrologic record using the Hydrologic Index Tool (Henriksen et al. 2006). Seven indices were selected that were representative of hydrologic conditions influenced by dam regulation in the region (McManamay et al. 2012) and had evidence of describing ecological responses to flow alteration (McManamay et al. 2013) (Table 1). Debate continues regarding how to appropriately characterize the hydrology of streams. Some advocate standardizing flow magnitudes to minimize the influence of river size (Poff 1996; Kennard et al. 2010) or regional differences that cause contrasting flow regimes (Olden et al. 2012), while others suggest that this approach obscures interpretation of true flow magnitudes (Chinnayakanahalli et al. 2011; Archfield et al. 2014). Because of the contrasting viewpoints, we characterized the multidimensional nature of streamflow in two different ways: (*i*) unscaled flow and (*ii*) scaled flow, where magnitude-related indices were standardized to control for river size. For scaled flow, mean annual flow (MA2) was divided by drainage area (e.g., mean annual runoff per km^2) and 1- and 90-day minimum flows were standardized by MA2 (dimensionless ratios, Kennard et al. 2010).

Fish assemblage sampling

Fish community data were compiled using records from the Tennessee Valley Authority (n = 54), Great Smokey Mountains National Park (n = 3), and our own surveys (n = 4) (Fig. 2). Methods are described in detail by McManamay et al. (2013). Depending on river size and species detection, fish communities were sampled within reaches five to ten times the bankfull width. Multiple gear types, including backpack electrofishing equipment, seines, dip nets, and boat shocking equipment, were used to ensure all habitat types represented were sampled (riffles, runs, pools, backwaters, and shorelines). Different gear types were used to most efficiently sample each habitat type using a grid-based design. Sampling efforts (i.e., spatial grids) for each habitat type continued until three successive runs failed to collect any new species. Sampling occurred during minimal flows to ensure unbiased capture efficiencies. All sites were sampled at least twice using similar methodology during 2000–2010.

We used fish assemblage information for the latest two sampling occasions for each site. As opposed to calculating relative abundances for each year, we calculated a composite relative abundance (rA) value as

$$\mathrm{rA}_i = \frac{(A_{i,t} + A_{i,t+1})}{\sum_{i=1}^{n}(A_{i,t} + A_{i,t+1})}$$

where A is the abundance for the ith species for the first and second year, t and t+1, respectively. We used this method because it minimizes the influence of individual year-to-year outliers.

We classified species by reproductive strategy and life history groups on the basis of information from FishTraits Database (Frimpong and Angermeier 2009) and analyses conducted in previous studies (McManamay and Frimpong 2015). Multiple studies have identified strong linkages among these trait groups and hydrology (Olden and Kennard 2010; Mims and Olden 2012; McManamay and Frimpong 2015). Fish were placed into one of three reproductive strategies, which included brood hiders, open-substratum spawners, and nest spawners (Balon 1975). Brood hiders hide or bury eggs within the substrate, whereas open-substrate spawners typically broadcast eggs over the substrate. In both cases, species display no parental care or guarding behavior. In contrast, nest spawners construct nests in which eggs are laid and guarded before, and many times after, hatching. Life history groups were taken from Winemiller and Rose (1992) and represent three endpoints in the trivariate continuum of tradeoffs among fecundity, generation time, and offspring survival. Equilibrium species have intermediate life spans and low fecundity but provide considerable parental care and have higher offspring survival. Opportunistic species are short-lived but reach sexual maturation very early; they have low offspring survival and no parental investment and typically spawn multiple times within a season. Periodic species are among the largest bodied fish; they are long-lived and take considerable time to reach sexual maturation but also have low parental investment. After controlling for phylogenetic inertia on life history traits, species were assigned to one of the three life history groups as described by McManamay and Frimpong (2015). After species were placed into trait groups, we calculated rA for each trait group for each site.

Statistical analyses

Principal components analysis

We used principal components analyses (PCA) of correlation matrices to reduce dimensionality in the seven flow and nine substrate variables. Variables were log(x+1)-transformed and centered to mean = 0 prior to analysis. We conducted separate PCAs for scaled and unscaled flow variables. For each of the three PCAs (substrate, scaled flow, and unscaled flow), we retained two principal components (PCs) and used them in MRT and path or SEM analysis. We tested for significant differences in predictor and response variables among regulation using Kruskal–Wallis tests, followed by nonparametric multiple comparisons.

MRTS

We used MRTs in the mvpart package in R (Therneau et al. 2014) as an exploratory technique to identify the importance of all predictor variables in partitioning fish assemblages on basis of similarities in rAs of reproductive strategies and life history groups. Similar to univariate regression trees, MRTs use predictor variables as splitting variables to maximize between-group sum-of-squares (SSD) between nodes relative to within-group SSD (i.e., groups of responses). However, in MRTs, SSD is minimized on the basis of distances between observations and the multivariate mean of each node. Thus, MRTs can be described as a form of constrained clustering of centroids (De'eath 2002). Because trees can become complex, cross-validation procedures are used to determine the most parsimonious tree that minimizes mean squared error and maximizes explained variance. MRTs clustered sites according to similarities in the proportions of life history groups and then identified the environmental variables that explained differences in those clusters. All variables, including flow PCs, substrate PCs, and regulation types, were included in the predictor ensemble in MRTs; however, the selection of final variables in trees was not constrained to follow any hypothesized hierarchical structure. Specifically, we hypothesized that the nature of dam regulation controlled the hydrogeomorphic conditions of river systems and thus could predictably influence the fish community (as supported by others, Mims and Olden 2013). To explicitly test this, we compared the amount of variation in trait groups explained by clusters with that explained entirely by regulation types by conducting a permutional multivariate analysis of variance (PMANOVA) using the adonis function in R (vegan package). PMANOVA is analogous to a nonparametric MANOVA except metric distance matrices are used to partition SSDs and permutations are used to develop pseudo F statistics (Anderson 2001).

SEM

To accompany the MRT analysis, we used a combination of classical path analysis and SEM to identify hierarchical pathways through which mechanisms influence individual fish assemblage components across spatial scales. Path analysis allows for estimation of direct and indirect relationships within complex systems on the basis of a priori hypothesized relationships between variables (Shipley 2002). Path analysis is particularly useful in ecological systems because it can be used to compare complex competing hypotheses about ecological relationships, given the structure of a dataset (Grace et al. 2010). In constructing path models, we imposed a hierarchical structure in which mechanisms operate unidirectionally across spatial scales (large-scale factors operating on instream factors) and laterally within scales (where appropriate) to influence stream fish communities. All hypothetical path diagrams imply that one large-scale variable, fragment length, directly affects fish community variables by limiting dispersal. We hypothesized that the remaining large-scale variables influenced fishes indirectly through instream variables. For each fish assemblage variable, we compared four general hypothetical pathways in which (*i*) flow and other instream factors affect fishes directly (Fig. 2A), (*ii*) flow affects fishes indirectly by influencing other instream variables that directly affect fishes (Fig. 2B), (*iii*) only flow directly affects fishes (Fig. 2C), and (*iv*) fishes are affected by instream habitat variables other than flow (Fig. 2D).

We conducted classical path analyses as a series of multiple linear regressions, as described by Freedman (2009). In classical path analysis, each multiple linear regression, depicted as a box with arrows going into it (Fig. 2), represents a submodel in the global path model for a given dependent variable. Accordingly, classical path analysis takes on the assumptions of multiple linear regression. To achieve approximate linearity, we arcsine(square root)-transformed proportions of life history and reproductive groups. We also modeled species richness; this variable was log-transformed. Habitat variables were already log(x+1)-transformed from the MRT analysis. To make all variables comparable to one another, we then scaled and centered all variables to mean = 0 and variance = 1. Categorical variables (drainage basin and regulation type) were coded as dummy variables — combinations of 1s and 0s that represent unique combinations for each category. For example, instead of one four-level categorical variable representing the four regulation types, we used three two-level categorical variables, in which 1 = the regulation type and 0 = the other three types. This is the appropriate way of coding categorical variables in path analysis (see Freedman 2009, pp. 103–104). We also used correlations to screen factors for egregious multicollinearity ($r > 0.70$).

To conduct path analysis, we began by modeling each fish assemblage component with a saturated submodel containing fragment length and all reach-scale variables. We then used the stepAIC function in the MASS package of R to conduct backward model selection and retain only factors that predicted the dependent variable at $\alpha = 0.05$. We repeated this process using large-scale variables to predict the reach-scale variables that significantly influenced the fish assemblage component. Both flow PCs were included as initial factors in these submodels (unless, of course, flow was the dependent variable). Backwards regression in this phase of path analysis provided an initial evaluation of competing hypotheses depicting the role of flow in the hierarchical structure (Fig. 2). This approach was ideal to coercing initial model structures and comparing global path models in an information-theoretic framework (Burnham and Anderson 2002) because the sheer number of variables would warrant too many models to compare subjectively (Hobbs and Hilborn 2006). To avoid redundancy among biotic variables, we modeled only rA of equilibrium and periodic life history groups, and only nest guarder and open-substratum reproductive groups; we also modeled species richness. In total, we conducted 10 separate path analyses and associated SEMs (five fish assemblage variables, with separate analyses for scaled and unscaled flow variables).

Classical path analysis is informative, but in itself gives no metric of overall model fit or stability. Accordingly, we subjected each final path model to SEM. SEM uses covariance matrix modeling to simultaneously assess the plausibility of all relationships in the proposed model. SEM can be more conservative than classical path analysis because "overidentified" models with too many weak paths will be unstable. Using the lavaan package in R (Rosseel 2012), we used each global path model as the initial SEM. To deal with modest sample size and heteroscedastic bivariate relationships, we fit SEMs using diagonally weighted least squares regression and based our inferences on robust (conservative) diagnostic statistics that are corrected for sample size. Models were evaluated on the basis of significance ($\alpha = 0.05$) of global χ^2 tests. In this case, adequate model fit is indicated by p values greater than the α value; failure to reject the null hypothesis indicates that the covariance structure in the specified model does not differ from the actual covariance structure, indicating a "statistically significant" model (Kline 2010). We sought SEMs that maximized explanatory power (i.e., retained as many paths as possible), as long as all paths were significant at $p \leq 0.05$ and the global model was stable ($p > 0.05$). To do so, we subjected each path model to SEM and sequentially removed the weakest paths until a stable model was achieved. This type of backwards selection is a common approach to identifying optimal SEMs (Blanc and Walters 2008; Spasojevic et al. 2014). To preserve degrees of freedom in SEMs and to avoid vague or nonsensical interpretations, we did not include lateral paths among large-scale factors in SEMs. All final SEMs contained at least five times fewer paths than observations, meeting a general rule of thumb for SEM sample size requirements (Petraitis et al. 1996). Finally, we estimated the cumulative effects of dam regulation (through instream factors) on each fish assemblage component by summing the products of standardized path coefficients leading from regulation type to the biotic variable (Shipley 2002).

Results

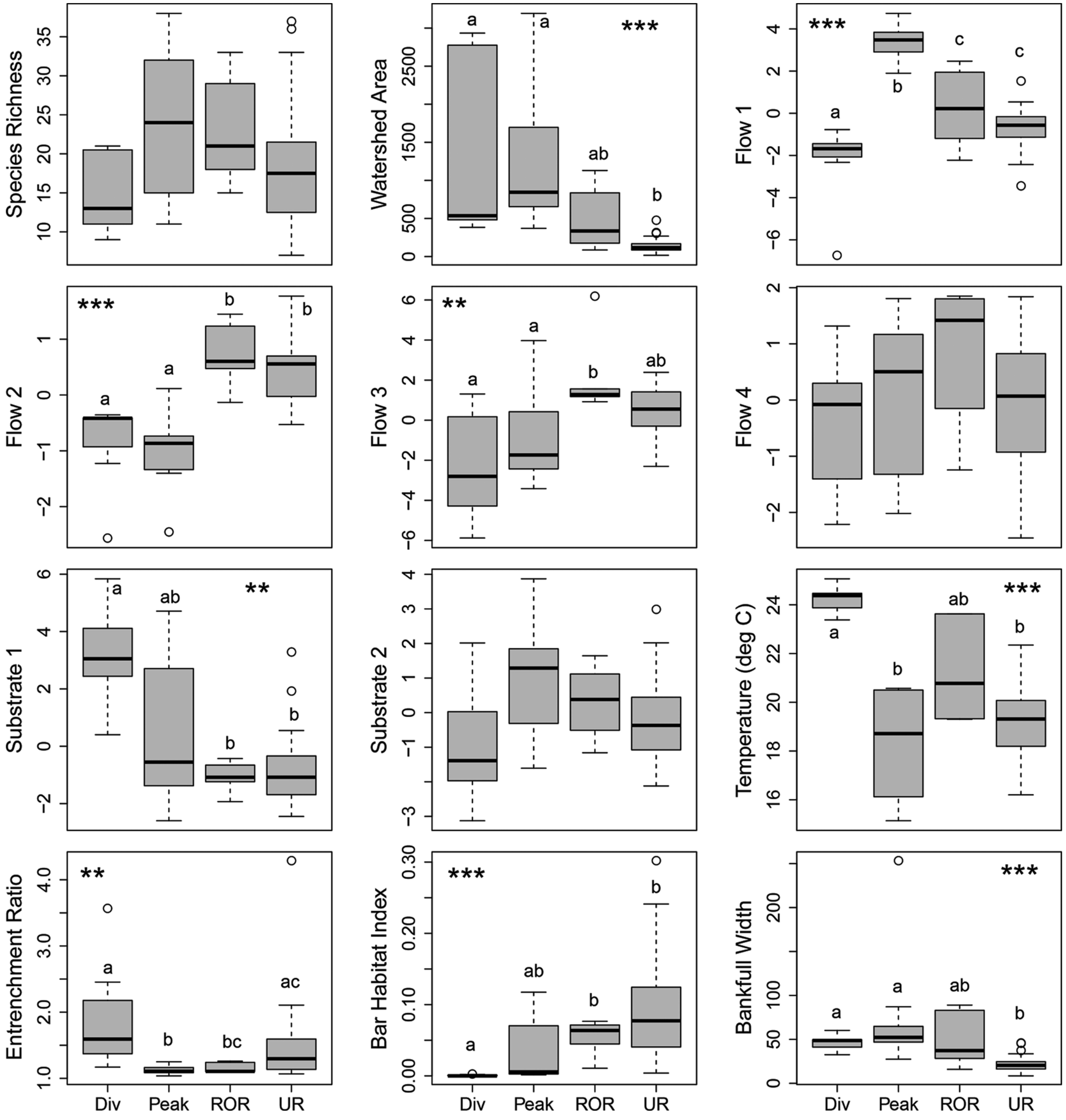
A total of 96 species were captured across all sites. The most common species included northern hog sucker (*Hypentelium nigricans*), central stoneroller (*Campostoma anomalum*), river chub (*Nocomis micropogon*), warpaint shiner (*Luxilus coccogenis*), rock bass (*Ambloplites rupestris*), and whitetail shiner (*Cyprinella galactura*) (in that order). Total richness ranged from 8 to 44 species at each site and averaged 22 species. Most species within the study area were equilibrium strategists (58), followed by periodic strategists (21), and opportunistic strategists (17). Composite rA followed a similar pattern with 67.0%, 16.5%, and 16.8% of individuals at each site, on average, being equilibrium, periodic, and opportunistic strategists, respectively. Reproductive strategies were more evenly distributed among species, with 32 species classified as brood hiders, 29 species at nest guarders, and 35 species as open-substratum spawners. However, rA did not mirror the frequency of species within reproductive strategies; brood hiders, nest guarders, and open-substratum spawners made up, on average, 55.1%, 28.7%, and 16.2%, respectively, of individuals at each site.

PCA

The first two PCs of unscaled flow variables explained 80% of the overall variation (denoted as flow-1 and flow-2). Increasing values of flow-1 represented higher flow magnitudes (MA2 (0.44), DL5 (0.44), and DL1 (0.43)) and more stable flows (MA3 (–0.39), FH6 (–0.35)). Higher values of flow-2 were characterized by higher baseflow indices (ML17 (0.52)) and lower low-flow frequencies (FL1 (–0.73)). For the standardized flow variables, the first two PCs explained 86.3% of the overall variation and were retained (denoted as flow-3 and flow-4). Baseflow index (ML17), high- and low-flow frequencies (FH6 and FH1, respectively), daily variability (MA3), and mean annual runoff (MA2 km^{-2}) all had high positive loadings (0.98, 0.98, 0.96, 0.95, 0.87, respectively) on flow-3, whereas 1-day (DL1) and 90-day (DL5) low flows had high positive loadings (0.87, 0.77, respectively) on flow-4. For substrate, the first two PCs explained 71.6% of the overall variation in the nine variables. Increasing values for the first substrate PC (denoted as substrate-1) represented increasing values in percent bedrock (0.42), D25 (0.42), D50 (0.41), and D75 (0.38) and decreasing values for percent gravel (–0.43). For the second PC (denoted as substrate-2), percent sand had a strong positive loading (0.50), whereas percent cobble and percent boulder had strong negative loadings (–0.55 and –0.34, respectively).

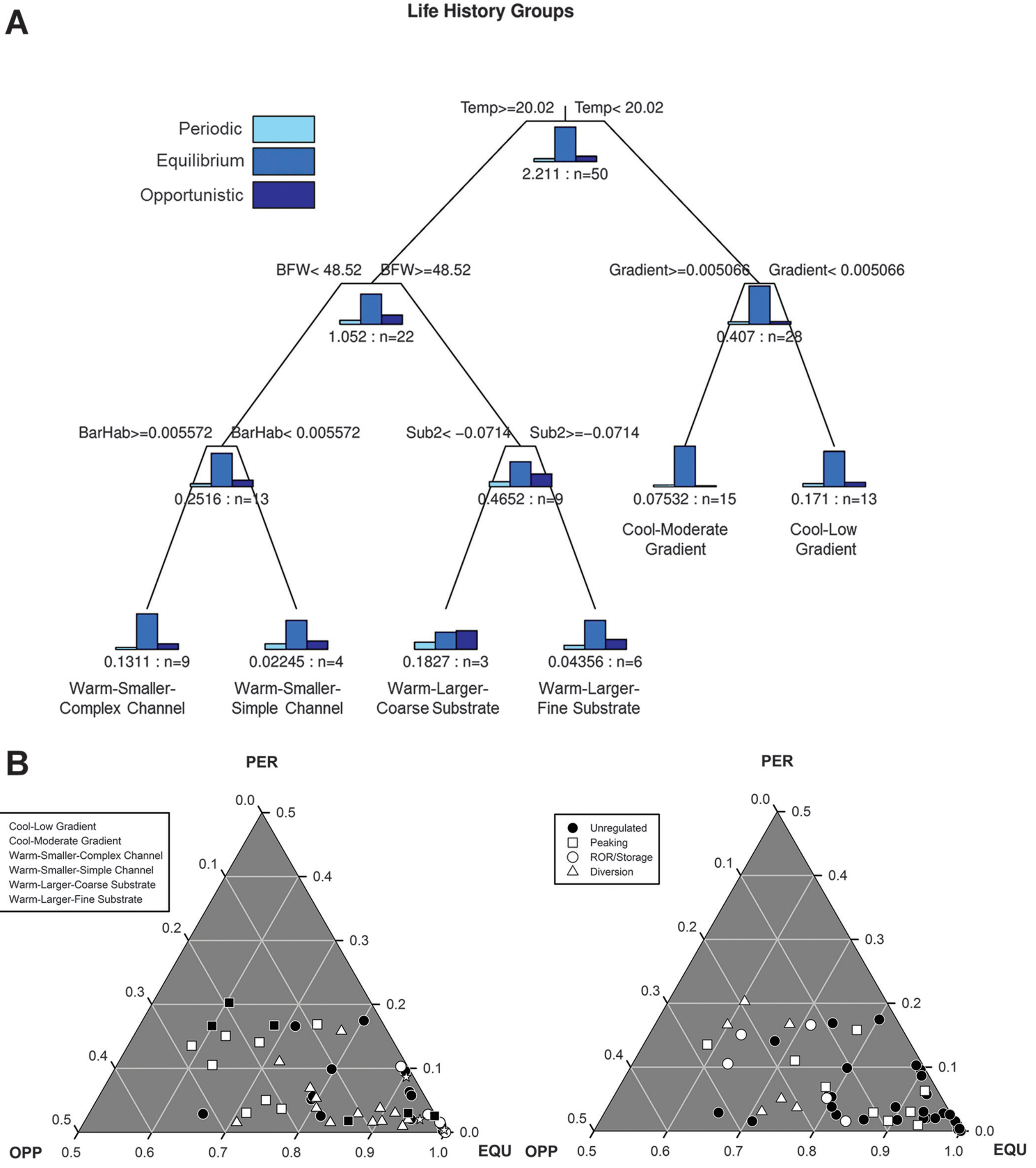
All but four predictor variables were significantly different among regulation types (Kruskal–Wallis, $p < 0.05$) (Fig. 3). Water-

Fig. 3. Distribution of species richness and a subset of predictor variables across dam regulation types using box and whisker plots. Boxes represent interquartile range, whereas whiskers represent 95th confidence interval. Black horizontal lines in boxes indicate median, and small open circles represent outliers. Different letters represent significant differences ($p < 0.05$) among regulation types. *, **, and *** indicate significant differences at the $p < 0.05$, 0.005, and 0.0005 levels, respectively. Div, diversion sites; Peak, peaking sites; ROR, run-of-river sites; UR, unregulated sites.



shed area and bankfull width were significantly lower in unregulated sites than peaking and diversion sites ($p < 0.05$). Several instream habitat variables displayed patterns among regulation types. Bar habitat was significantly higher in unregulated and ROR–storage sites than diversion sites ($p < 0.05$). Diversions had significantly higher entrenchment ratios to peaking and ROR–storage sites but not unregulated sites ($p < 0.05$). Temperature was significantly lower in peaking sites than in diversion sites but not significantly different among other regulation types ($p < 0.05$). Substrate-1 was significantly higher (higher percent bedrock, coarser substrate) in diversion sites than ROR–storage and unregulated sites but not peaking systems ($p < 0.05$). Flow-1 was significantly

Fig. 4. (A) Multivariate regression trees (MRT) predicting life history groups of fish assemblages at sampling sites. Numbers below each node represent error rate and number (*n*) of observations. (B) Ternary plots display the distribution of sites within the tri-life history continuum on the basis of MRT results (left) and different regulation types (right). BFW, bankfull width; Temp, temperature; BarHab, Bar habitat index; Sub2, substrate 2; PER, periodic; EQU, equilibrium; OPP, opportunistic; ROR, run-of-river.



lower at diversion sites (lower flow magnitudes) than other sites, whereas peaking sites had the highest flow-1 values (Fig. 3). Flow-2 and flow-3 were significantly lower in diversion and peaking sites than ROR–storage sites and not significantly different from unregulated sites (Fig. 3).

MRTs

MRTs explained 72% of variation in life history groups (six terminal nodes) and 52% of variation in reproductive strategies (five terminal nodes) (Figs. 3–4). Temperature and gradient were present in both trees but also served as initial parent nodes, which indicates they explained more variation than other variables. Flow was only represented in the reproductive strategy MRT tree by flow-2, an indication of baseflow conditions. Colder systems were dominated by equilibrium species, whereas the abundance of periodic and opportunistic species was variable in warmer systems, depending on stream size, morphological conditions, and substrate (Fig. 4). Brood hiders were strongly affiliated with higher gradients, whereas open-substratum and nest-guarder abundance depended on temperature, baseflow conditions, and stream size (Fig. 5). Patterns in traits were evident among both MRT clusters and regulation types; however, regulation types explained less variation than MRT trees. Regulation types explained 34% of variation in life history groups ($F_{[3,46]} = 7.74$, $p = 0.003$) and 19% of variation in reproductive strategies ($F_{[3,46]} = 3.68$, $p = 0.012$).

SEM

Evidence provided by path analysis and SEM suggests that no single instream habitat factor dominated prediction of stream fish community variables. In path models with both scaled (Fig. 6A) and unscaled (Fig. 6B) flow variables, fish community variables were predicted mainly by fragment length, temperature, substrate PCs, and flow PCs. Although weak relationships between flow and significant instream habitat variables (namely temperature and substrate PCs) were evident in preliminary path analyses, they were not strong enough to be included in final SEMs.

Dam regulation was not consistently present in pathways affecting specific fish assemblage components, but natural large-scale predictors were typically present. For instance, only five of the ten SEMs contained significant paths from regulation type to biotic response variables (regardless of flow scaling). However, only one fish assemblage variable (percent equilibrium species) had regulation types as the only important large-scale factor. Instead, eight of ten SEMs contained natural large-scale predictors (most notably gradient, interbasin variability, and watershed area); five of those had no regulation type variables at all (Figs. 6A and 6B).

In both scaled and unscaled path models, dam regulation had cumulative negative effects on all fish community variables by influencing instream factors (Total effects, Table 2). However, diversion projects and ROR–storage regulation had positive indirect effects on species richness by increasing temperature. For diversion dams, these positive effects were countered by large decreases in flow magnitude (flow-1) (Table 2). In this case, the positive indirect effects on species richness through temperature were weak compared with the strong negative indirect effect through flow — hence the cumulative negative effect of dam regulation on species richness in the SEM with unscaled flow variables.

Discussion

Our results suggest that in the Upper Tennessee River Basin, both natural large-scale factors and dams operate to influence fish assemblages through a few key instream habitat variables, not just flow. Although flow displayed direct and indirect relationships with biotic responses, both MRTs and SEMs suggested that other instream habitat factors, specifically temperature and substrate, had equal, and often stronger, effects on fish assemblage composition. However, the nature of direct and indirect relationships between flow and biota depended on how flow was defined (i.e., scaled or unscaled). Specifically, if river size is not accounted for in ecohydrologic studies, important hydrologic determinants of ecological composition may be overlooked. While the strength, nature, and extent of how dams have offset processes vary widely according to different river systems (Ward and Stanford 1983), the consistent observation within this study is that the hierarchical organization of river systems is altered and flow is disconnected from other biophysical processes. Specifically, we found that the hierarchical arrangement of large and local factors within rivers in our study area represent hypotheses A and B in Fig. 2, where large-scale factors (including dam regulation) induce changes in instream factors, which then influence the composition of fish assemblages. While flow may directly influence biota, it does not exert changes on other instream factors; this is the major pathway in which the natural hierarchy has been modified in our study. An important consideration, however, is that the nature of changes in the river hierarchy due to dam regulation may vary geographically and across different types of dams, as our study only reflects a specific region and primarily hydropower dams; thus care must be taken in widely applying our results. Nonetheless, the results of this study suggest that the role of physiochemical drivers on fish assemblages in regulated river systems is complex and multidimensional, and this view is required to ensure regulated river management is relevant to fish community needs.

The regulated river hierarchy

Local fish assemblages are shaped by habitats whose structure and complexity are governed by factors operating at larger scales, such as geomorphic constraints on valley morphology. However, the relative importance of local versus large-scale factors is a matter of perception, which is an artifact of the scale of any study (Jackson et al. 2001). Distinct flow regimes vary regionally with climate and exert strong controls on the composition of species pools (McManamay and Frimpong 2015). However, the extent of our study occurred within the same hydroclimatic context, and we were evaluating patterns in local communities as opposed to species pools; thus the importance of flow, or lack thereof, must be couched within this spatial extent.

We hypothesized that large-scale factors influence local fish assemblages directly, such as fragmentation, or indirectly by controlling instream habitat. Assuming the hypothesized structure is correct, the question of hierarchical organization then becomes, What is controlling the physical structure of instream habitats — stream flow or other factors? At the scale of valley segments, geomorphic controls may have stronger influences on habitat formation than differences in flow regimes within a region of similar climate. For example, the ability of a river channel to adjust its morphology in relation to flow will depend upon the alluvial character of the river and associated geomorphic constraints (i.e., ability to aggrade and degrade; Trush et al. 2000). In contrast to alluvial river systems (i.e., those with mobile particles), flow regimes may exert less control over channel morphology in nonalluvial systems, at least over the course of decades (Wohl 2010). For example, bedrock outcrops were present in the river channel at the majority of our sites (76% all sites, 63% unregulated sites); this is an artifact of longer weathering of ancient mountains and valleys in the Blue Ridge physiographic province (Rast 1989) and the historic removal of wood (Roni et al. 2015). Ultimately, this suggests confined valleys and geomorphic controls impose constraints on river channel geometry and habitats. Not surprisingly, gradient was a strong organizer of fish communities in both MRT models and by operating indirectly through substrate in path models. Likewise, gradient was a dominant factor controlling stream habitat structure in Piedmont streams of the Southeastern US (Walters et al. 2003) and a strong predictor of fish assemblage structure in the southeastern Appalachians (Kirsch and Peterson 2014).

Flow regimes

The perceived role of flow in structuring river communities largely depends on how flow is measured and summarized. Flow accumulates with drainage area, creating more habitat, niche space, and stability. Thus, flow magnitude is expected to have strong positive effects on richness (Xenopoulos and Lodge 2006),

Fig. 5. (A) Multivariate regression trees (MRTs) predicting reproductive strategies of fish assemblages at sampling sites. Numbers below each node represent error rate and number (*n*) of observations. (B) Ternary plots display the distribution of sites within the reproductive strategy continuum based on MRT results (left) and different regulation types (right). Temp, temperature; WSAI, log-transformed watershed area; BHD, brood hider; NST, nest guarder; OPS, open substratum.

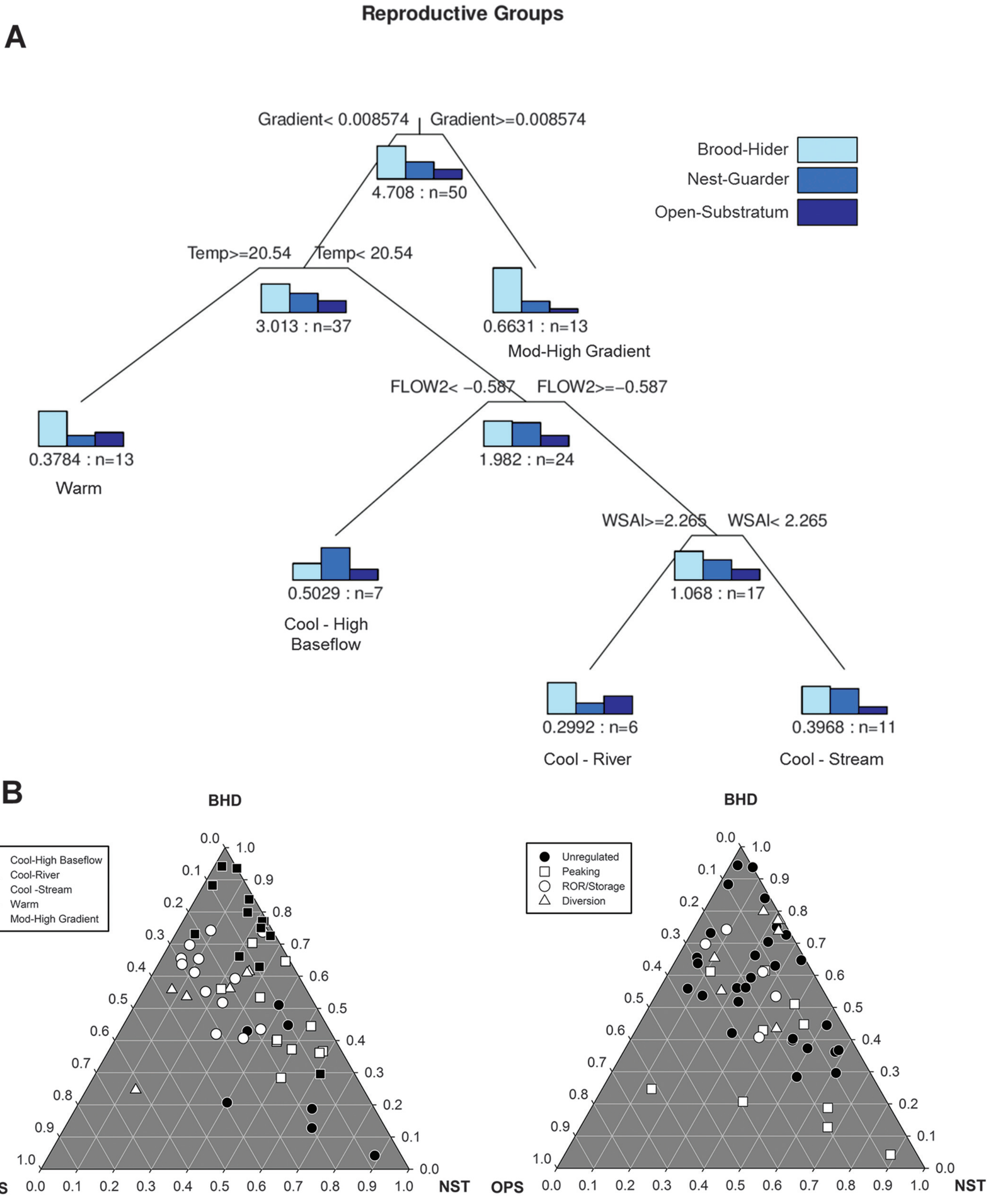


Fig. 6. Ten structural equation models (SEMs) depicting the relative effects of large-scale factors and instream habitat on five biotic response variables. SEMs contained either scaled (A) (i.e., standardized by mean daily flow or watershed area) or unscaled (B) instream flow predictors. Solid lines represent positive effects, and dashed lines indicate negative effects. Boxes on each line represents a parameter estimate (standardized regression coefficient) bounded by a standard error. Global model statistics are shown in the box containing each biotic response variable. Models were evaluated on the basis of global χ^2 tests at $\alpha = 0.05$. SEMs with global p values >0.05 were considered statistically significant (Kline 2010). An asterisk next to the p value indicates that the path was significant at $\alpha = 0.05$, although the global model was not significantly stable (i.e., $p \leq 0.05$).

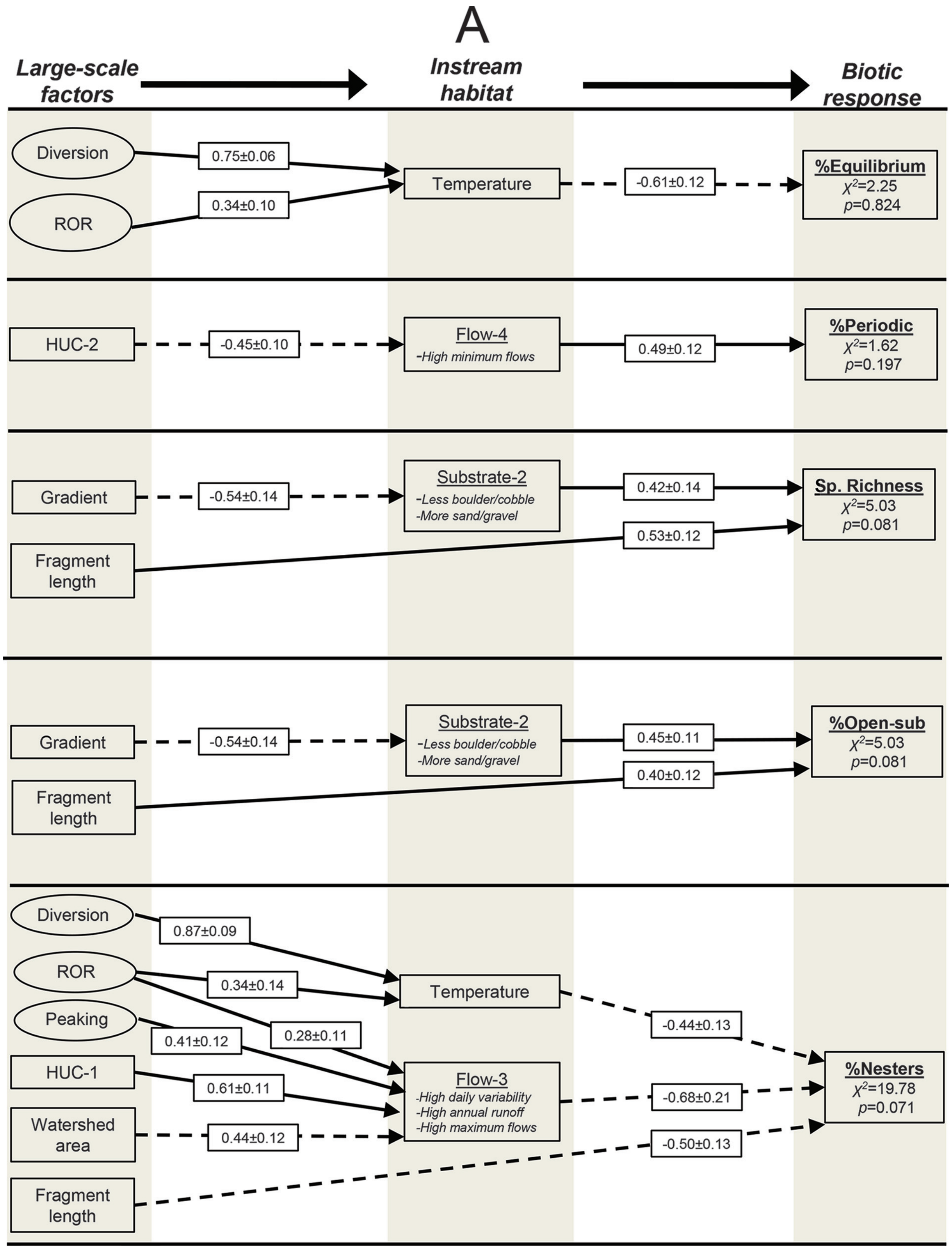
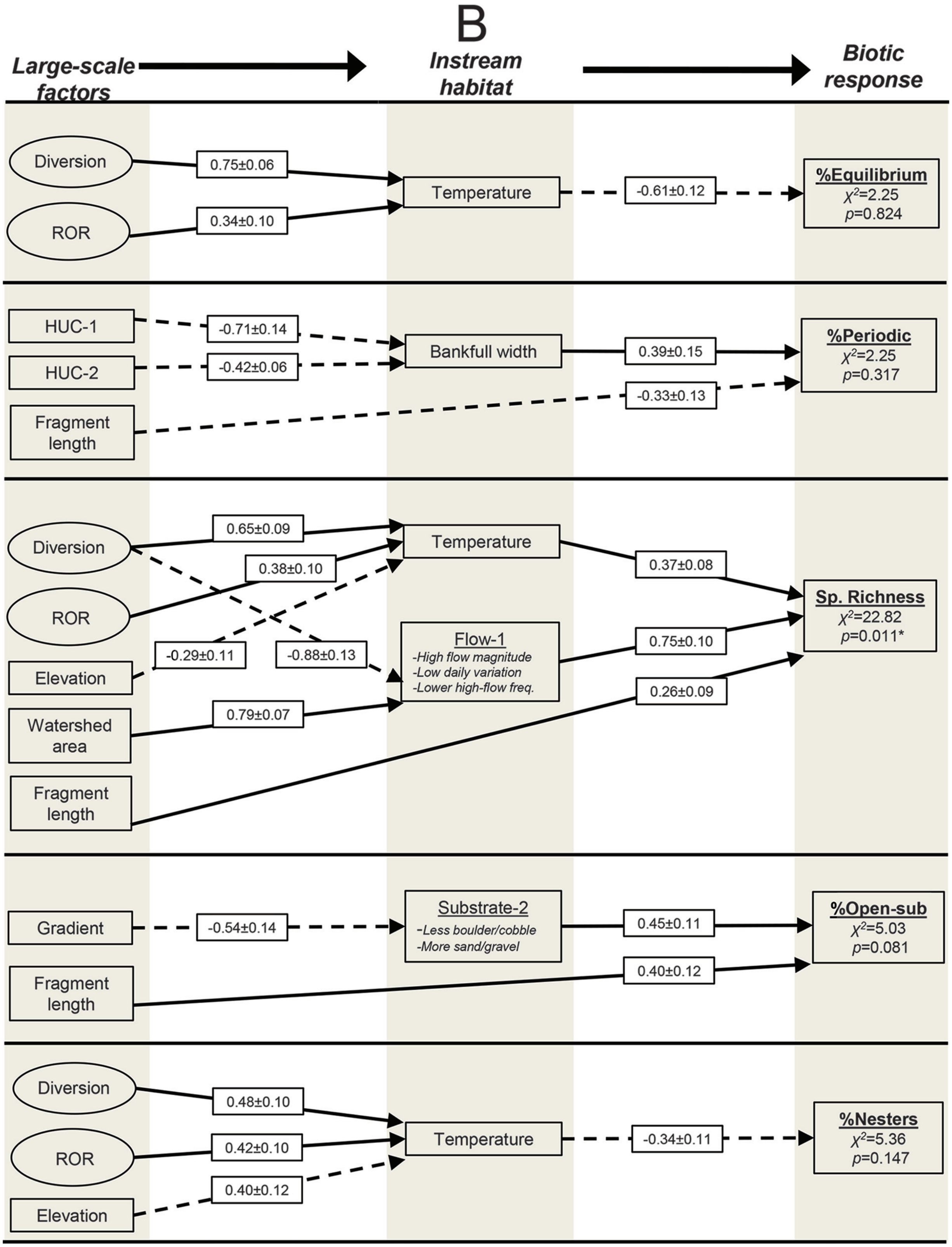


Fig. 6 (*concluded*).



as we observed in the unscaled flow model. However, unstandardized flow magnitudes may not provide true measures of flow variability among streams and hence lead to incorrect conclusions regarding the importance of hydrology on fish communities. For example, two pathways were evident in the scaled flow model but unobserved in the unscaled model (Figs. 6A and 6B; we describe the ecological meaning of these relationships later). In the scaled models, minimum and high flow values are ratios and more indicative of stability with respect to average conditions as opposed to raw volumes. Because unregulated streams in our study area

Table 2. Indirect effects of three regulation types (diversion projects, run-of-river (ROR)–storage, and peaking) on proportional representation of life history and reproductive groups, and species richness (summarized as "biota" below), at 50 sites on tributaries to the Upper Tennessee River, USA.

	Models with scaled flow variables			Models with unscaled flow variables		
Path	% Nesters	% Equilibrium	Richness	% Nesters	% Equilibrium	Richness
Diversion → temperature → biota	−0.38	−0.46	—	−0.16	−0.46	0.24
ROR–storage → temperature → biota	−0.15	−0.21	—	−0.14	−0.21	0.14
ROR–storage → flow-3 → biota	−0.19	—	—	NA	NA	NA
Peaking → flow-3 → biota	−0.28	—	—	NA	NA	NA
Diversion → flow-1 → biota	NA	NA	NA	—	—	−0.66
Total	**−1.00**	**−0.66**	**0.00**	**−0.31**	**−0.66**	**−0.28**

Note: Values represent products of standardized beta coefficients for each regression path (indicated by arrows) from flow regulation, through an instream habitat variable, to a biotic variable, and were estimated using structural equation modeling (SEM). Total effects (in bold) represent sums of values (products of coefficients) for each biotic response variable. Regulation type was not a significant predictor in either SEM predicting proportions of periodic strategists or open-substratum species, thus, these groups are not reported below. "NA", suggests a given path is not applicable depending on whether flow was scaled or not.

had considerably smaller watersheds than those in regulated systems, determining the effect of dam regulation on flow regimes, and any associated effects on biota, requires careful inspection when using unstandardized flow magnitudes. We recommend that future work should account for the pervasive effect of watershed area, whether by standardizing flow or explicitly including it in predictive models.

Unscaled and scaled flow PCs described different aspects of the flow regime and displayed different relationships with biota; however, there was no evidence that flow was structuring other instream habitat variables. Unscaled flow PCs typically represented river size (flow-1) or conditions in baseflow and extreme-flow-frequency (flow-2). As expected, species richness increased with increasing flow magnitudes (flow-1); that is, more species exist in larger rivers (Xenopoulos and Lodge 2006). In contrast, scaled flow PCs represented variability, runoff per unit drainage area, and high-flow flows relative to average conditions (flow-3) or minimum flows relative to average conditions (flow-4). Periodic species are typically large-bodied, slow-growing fishes adapted to living in rivers with predictable but seasonally fluctuating flow (Winemiller 2005). Because high flow-4 suggests that channels remain watered throughout the year, its positive relationship with periodic species is in accordance with life history theory. Negative effects of flow-3 on nest guarders also makes intuitive sense, as higher parental care would seem advantageous in stable environments with lower variation. However, the opposite was found in a study across the US where nest-guarding fishes were affiliated with high daily flow variation (McManamay and Frimpong 2015), which was likely due to nest-guarding behavior allowing flexibility in the selection of optimal nest habitats in protected areas (Lukas and Orth 1995; Peoples et al. 2014).

One limitation of our analysis was that we did not account for subdaily flow variation, which may have elucidated stronger relationships among flow, habitats, and fish. For example, peaking operations induce rapid changes in flows on the scale of minutes and are likely to dramatically influence fish communities (Cushman 1985). In addition, the majority of dams assessed in our study were hydropower facilities, compared with only two flood-control dams and one water supply dam. Accordingly, this likely influenced the hydrologic variables deemed important in our study and our conclusions. For example, we did not include flow timing components in our analysis, as timing did not show consistent responses to dam regulation in our region (McManamay et al. 2012). However, flood-control facilities are more likely to influence timing components of flow regimes as they store water during high-flow seasons to purposefully dampen flood events. Thus, our conclusions must be considered in light of the regulatory context.

Dam regulation

We observed different changes in flow, temperature, and biotic responses according to regulation types; however, the most predominant pathway between dam regulation and biota was via temperature alteration. Different temperature effects from dam regulation result from different dam structures (Olden and Naiman 2010). For example, peaking dams in the study area are bottom-release structures leading to cold-water releases, whereas diversion dams and ROR dams have surface release or have shallow-surface intakes, respectively, and result in elevated temperatures. Diversion dams may exaggerate elevated temperature conditions from surface releases by simultaneously reducing thermal buffering capacity via reductions in flow (McManamay et al. 2013). The ecological effects of temperature alterations from dams have been well-documented (Krause et al. 2005; Lessard and Hayes 2003).

Although peaking dams had lower temperatures, there was no significant indirect pathway between peaking operations, temperature, and biota. Mims and Olden (2013) reported increases in equilibrium species due to cold-water releases from dams. In accordance with these findings, our results suggested that diversion and ROR dams decreased equilibrium species by increasing temperatures. Likewise, Anderson et al. (2006) also found that diversions had the largest negative effects on equilibrium species. Equilibrium species are small-bodied fishes with small clutches that display considerable parental care to optimize juvenile survivorship (Winemiller and Rose 1992). Although equilibrium strategists prefer stable hydrologic environments (Tedesco et al. 2008; Mims and Olden 2012), they also display *K*-selected population growth, a life history strategy adapted towards resource-limited environments (Winemiller and Rose 1992). Thus, increased temperatures may alleviate resource limitations or exceed physiological tolerances for many equilibrium species in the region.

Elevated temperatures below diversion and ROR dams also decreased nest guarders and increased species richness. While nest guarders include most centrarchids, the group also includes several species, including sculpins (*Cottus*), madtoms (*Noturus*), several darters (*Etheostoma*), and longnose dace (*Rhinichthys cataractae*, substrate chooser), all of which prefer cooler temperatures and become rare or absent in diversions and tailwaters below ROR dams. However, the positive effect of diversion and ROR dams on species richness via elevated temperature (in unscaled model) was unexpected and likely an artifact of increasing drainage area at some sites; however, the relationship was too weak to include in the final model.

Evidence of flow-mediated relationships between dam regulation and biotic responses was also observed but was less abundant than temperature relationships. Diversion dams reduced flow magnitudes and exerted strong negative effects on species richness, which countered any positive effects from increased temperature (Table 2). Losses of fish species are expected with reduced habitat area and have been reported elsewhere (Anderson et al. 2006; Poff and Zimmerman 2010). In contrast, peaking and ROR dams increased flow-3 (increasing instability), which decreased nest-guarding fishes. This made intuitive sense, as nest guarders rely on stable environments, including slack waters, to construct and guard nests (Lukas and Orth 1995).

Landscape and habitat considerations

When considering the role of any instream habitat variable on fish community structure, a larger-scale landscape context is essential to understanding causal mechanisms of species presences and absences (Fausch et al. 2002). In addition to local habitat alterations, dams also create discontinua in stream networks by inhibiting fish movement among habitat patches. Thus, habitat connectivity must be taken into account to fully understand effects of dam regulation on fishes. For example, the presence of large-bodied migratory fishes like the redhorses (*Moxostoma*) may be unassociated with localized habitat disturbances if fragment lengths are not sufficient to support yearly spawning migrations (Cooke et al. 2005). Redhorse species richness was positively related to fragment length and completely absent from highly fragmented watersheds of the Grand River, Ontario (Reid et al. 2008). In our study, total species richness was positively related to fragment length. In light of this, the negative effect of fragment length on periodic species was unexpected. This resulted from a few highly fragmented sites with high abundances of northern hog sucker, the only catostomid species detected at those sites. Although migratory behavior is common among many catostomids, northern hog sucker typically exhibit movements less than a kilometre (Matheney and Rabeni 1995).

Fragmentation has impacts on many species besides large-bodied fishes. Colonization potential is directly related to migratory movement rates, which may be unrelated to body size (Albanese et al. 2009). For example, Breen et al. (2009) documented mottled sculpin (*Cottus bairdii*) dispersing over 500 m in a year. Likewise, darters have also been shown to migrate extensive distances (Roberts and Angermeier 2007) and are negatively affected by fragmentation (Beneteau et al. 2009; Kashiwagi and Miranda 2009). Declines in cyprinid fish populations, especially those requiring considerable drift distances for nondemersal eggs, have also been linked to habitat fragmentation by dams (Han et al. 2008; Hoagstrom et al. 2008; Perkin and Gido 2012).

While substrate-mediated biotic responses to dam regulation were not included in final models, our results suggest that dam regulation is influencing substrate conditions (e.g., Fig. 3). In addition, the prevalence of substrate in both MRTs and SEM models suggests that substrate size is an importance determinant of fish community composition. For example, open-substratum spawners showed strong positive associations with the abundance of sand and (or) gravel substrates (substrate-2), as these species need finer substrates for broad casting eggs (Balon 1975). In addition, species richness was positively related to the abundance of finer substrates, suggesting that substrate armoring by dams (by capturing bedload) would lead to losses in fish species. Although substrate was hypothesized to be structured by all large-scale drivers, channel gradient was the predominant determinant of substrate size in rivers in our study, as reported by others (Walters et al. 2003). Compared with the number of studies of invertebrates, there is a paucity of studies directly linking the effects of dams to substrate-mediate responses of fish reproductive guilds and species richness (McManamay et al. 2013).

Dams and fish life history theory

Predicting fish life history responses to dam regulation on the basis of generalizations in dam behavior (usually regarding hydrology) may be misleading, since these generalizations may or may not accurately reflect the true multidimensional nature of stream environments and the pressures they exert on stream fish (see Mims and Olden 2013). Of these generalizations, the most common is that dams reduce hydrologic variation and increase stability (Magilligan and Nislow 2001; Poff et al. 2007). Under these selective pressures, equilibrium strategists are predicted to increase, whereas opportunistic strategists are predicted to decrease (Winemiller 2005), and multiple studies have shown support for this concept (Olden and Kennard 2010; Mims and Olden 2012; McManamay and Frimpong 2015). The problem, however, is not the theory but the over-generalized view of dams (i.e., that dams act as stabilizing agents that homogenize variable environmental conditions). While many dam operation strategies can produce this pattern, many actually have the opposite effects. Diversion dams actually increase variation, making streams more unpredictable (Stromberg et al. 2007). Although peaking dams tend to increase seasonal stability, subdaily fluctuations cause abrupt hydrologic changes over a period of minutes (Cushman 1985). Temperature, sediment, and morphological dynamics create even more uncertainty in predicting ecological responses to dams.

In terms of overall model averages (regardless of scaled or unscaled flow), dam regulation decreased equilibrium species but increased opportunistic species, opposite than expected on the basis of generalities in dam-induced hydrologic effects. In addition, there were no consistent effects of dam regulation on periodic species. Mims and Olden (2013) also reported ecological responses to dams not in accordance with life history theory. Equilibrium strategists were more predominant below dams despite net reductions in hydrologic predictability. Mims and Olden (2013) suggested this was a result of hypolimnetic releases from dams as opposed to hydrology-related effects. Negative responses by equilibrium species to elevated temperatures suggest consistent physiological constraints (as opposed to ecological preference) and an important consideration in life history adaptation to dam regulation. One challenge in addressing the biophysical effects of dam regulation is that dams simultaneously influence different habitat variables, which at times, lead to opposite effects on biota. For example, diversion dams increase temperatures, which are associated with positive effects on richness, but at the same time, diversion dams reduce flow magnitudes, leading to losses in species (Table 2). Hence, a multivariate and hierarchical view of processes affected by dam regulation should be considered when evaluating ecological responses and associated management regimes. Nonetheless, life history theory serves as a robust framework for testing fish responses to dam regulation.

Implications for regulated river restoration

We suggest that for regulated river restoration to be effective, multiple facets of river ecosystems should not only be considered, but restored. Although upfront expenses can be high, altering the physical structure of intakes at dams to pull water from different stratified layers of reservoirs may be required to provide suitable temperature conditions for fish assemblages (Krause et al. 2005; Olden and Naiman 2010). These structural changes can be used in conjunction with mimicking more natural flows, as the combined effects of flow and water quality on biota has shown more promise than enhancing flows alone (Bednarek and Hart 2005). In situations of low dissolved oxygen, spill gates or intakes have been retrofitted with oxygen diffusers to enhance water quality conditions (Bednarek and Hart 2005). Across the US, it is estimated that 25% of sediment typically transported in streams is captured in impoundments (Renwick et al. 2005). Given the consistent geomorphic responses to dam regulation (Grant 2012), it would seem that sediment restoration would be commonplace. However, with the exception of endangered salmonid recovery efforts in the western US (Kondolf 1997), the impact of dam-induced substrate alterations on fish assemblages has likely been underestimated, since substrate restoration below dams is uncommon in the eastern US (McManamay et al. 2010). Because the conservation of many freshwater mussels (Vaughn and Taylor 1999) and endemic minnows (Johnston 1999) is directly tied to substrate conditions, substrate restoration should not be overlooked as an important component mitigating the effects of dam regulation. On the basis of estimates of a river's carrying capacity and desired sediment regime, washed gravel and sediment substrates have been periodically augmented to regulated reaches either through direct placement in channels (Kondolf 1997) or passively along embankments in areas of high entrainment potential (McManamay et al. 2010).

Petts (1984) originally suggested the hierarchy of habitat-related impacts stemming from dam regulation, varying from primary to tertiary effects. First-order effects include hydrology, water quality, and sediment regimes (we add fragmentation here); secondary effects include fluvial morphology and substrate; and tertiary effects include biotic responses. This model is generally accepted as the predominant conceptual framework to visualize the complex biophysical responses to dam regulation (Jorde et al. 2008; Burke et al. 2009). Herein, we emphasize the importance of understanding not only indirect pathways between flow and fish responses but also direct pathways, such as the effects of temperature on biota. An additional layer of complexity to consider in restoration is biological feedback mechanisms, such as disrupted food web structure (Orth 1987). To ensure that the conceptual understanding of dams on river systems translates into effective river restoration, approaches are needed that harness as much information as possible and develop hierarchical modeling platforms to support quantitative predictions (Kirsch and Peterson 2014; Webb et al. 2015).

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