

Hydrologic filtering of fish life history strategies across the United States: implications for stream flow alteration

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Abstract. Lotic fish have developed life history strategies adapted to the natural variation in stream flow regimes. The natural timing, duration, and magnitude of flow events has contributed to the diversity, production, and composition of fish assemblages over time. Studies evaluating the role of hydrology in structuring fish assemblages have been more common at the local or regional scale with very few studies conducted at the continental scale. Furthermore, quantitative linkages between natural hydrologic patterns and fish assemblages are rarely used to make predictions of ecological consequences of hydrologic alterations. We ask two questions: (1) what is the relative role of hydrology in structuring fish assemblages at large scales? and (2) can relationships between fish assemblages and natural hydrology be utilized to predict fish assemblage responses to hydrologic disturbance? We developed models to relate fish life histories and reproductive strategies to landscape and hydrologic variables separately and then combined. Models were then used to predict the ecological consequences of altered hydrology due to dam regulation. Although hydrology plays a considerable role in structuring fish assemblages, the performance of models using only hydrologic variables was lower than that of models constructed using landscape variables. Isolating the relative importance of hydrology in structuring fish assemblages at the continental scale is difficult since hydrology is interrelated to many landscape factors. By applying models to dam-regulated hydrologic data, we observed some consistent predicted responses in fish life history strategies and modes of reproduction. In agreement with existing literature, equilibrium strategists are predicted to increase following dam regulation, whereas opportunistic and periodic species are predicted to decrease. In addition, dam regulation favors the selection of reproductive strategies with extended spawning seasons and preference for stable conditions.

Key words: classification frameworks; dams; ecohydrology; environmental flows; fish reproductive strategies; fish traits; flow–ecology relationship; hydrologic alteration.

INTRODUCTION

Lotic fish have developed life history strategies adapted to the natural variation in stream flow regimes (Poff et al. 1997, Bunn and Arthington 2002). The natural timing and magnitude of flooding establishes the template on which riverine habitats are created and then maintained (Trush et al. 2000) and provides behavioral cues for the initiation of spawning and seasonal migrations (Nesler et al. 1988, King et al. 1998). Likewise, the magnitude and duration of high flows determines the accessibility of spawning habitat (Grabowski and Isely 2007) and juvenile rearing habitats for fish (Leitman et al. 1991, Light et al. 1998), whereas the magnitude and duration of low to moderate flows governs the stability and suitability of feeding and resting habitats and associated changes in stress (Freeman and Grossman 1993, Peterson and Jennings 2007). Studies have suggested that hydrology forms the habitat template (Schlosser 1987, 1990) or hierarchical

filter (Jackson and Harvey 1989, Tonn 1990, Poff 1997), which organizes trade-offs among adaptive strategies within fish populations and assemblages. The wide range of natural flow conditions across the U.S. continent (Poff 1996) exerts different selective pressures that shape fish life history and reproductive strategies and result in regionally distinct fish assemblages (Southwood 1988, Olden and Kennard 2010, Mims and Olden 2012).

Assessments of the role of hydrology in structuring fish assemblages has been more common at the local or regional scale (e.g., Pyron and Lauer 2004, Knight et al. 2008) with very few studies conducted at the continental scale (e.g., Carlisle et al. 2011). Furthermore, quantitative linkages between natural hydrologic patterns and fish assemblages are rarely used to make predictions of ecological consequences of hydrologic alterations. If fish assemblages vary predictably with natural variation in hydrology at large scales, then logically, one would presume that anthropogenic-induced changes in hydrology may predictably influence fish assemblage composition. Thus, two questions remain to be answered: (1) what is the role of hydrology in structuring fish assemblages at large scales? and (2) can predictive

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relationships between fish assemblages and natural hydrology be utilized to predict fish assemblage responses to hydrologic disturbance?

Pinpointing the role of hydrology in structuring fish assemblages is complicated because hydrology operates at multiple temporal and spatial scales (Poff et al. 1997, Olden et al. 2012) and is interrelated with many other determinants of fish assemblage composition (Marsh-Mathews and Mathews 2000). Thus, developing models to predict how hydrology may shape regional species pools requires accounting for other abiotic variables. However, the hierarchical nature of how abiotic factors filter regional species pools through selective pressures to shape the composition of local communities is still poorly understood (Jackson et al. 2001). Because predicting the presence of individual species in local communities is complicated by uncertain evolutionary processes along phylogenetic lineages and by local abiotic controls, it is advantageous to examine the changes in communities via a traits lens because traits consolidate information across many taxonomic groups into common adaptive strategies (Frimpong and Angermeier 2009, 2010*b*). Species of similar phylogenetic lineage share characteristics and constraints through common evolutionary descent (i.e., phylogenetic inertia); thus, phylogeny should be accounted for in analyses evaluating variation in species' life histories with environmental variables. Traits provide a mechanism to account for phylogeny while inferring species' adaptation to environmental gradients. Multiple studies have used fish traits to determine the role of habitat, landscape filters, and anthropogenic disturbances in shaping fish communities (Schlosser 1990, Winemiller and Rose 1992, Goldstein and Meador 2004, Grouns 2004, Blank et al. 2007).

With specific regard to hydrology–trait relationships, life history groups and habitat-preference guilds have received the most attention (Poff and Allan 1995, Pyron and Lauer 2004, Blank et al. 2007, Tedesco et al. 2008, Olden and Kennard 2010, Mims and Olden 2012, 2013), with fewer applications to reproductive strategies (Craven et al. 2010, Carlisle et al. 2011). Winemiller and Rose (1992) originally proposed three major endpoints (periodic, equilibrium, and opportunistic) in the life history strategies of fish species representing a continuum of tradeoffs among survival, growth, fecundity, and parental care. The trivariate space occupied by a fish is an indication of the selection pressures of its environment, primarily driven by hydrologic variation (Winemiller 2005). For example, periodic strategists grow to large sizes, have late sexual maturation, and have high fecundity for successfully reproducing under suitable conditions (Winemiller 2005), all as an adaptation to rivers with predictable, but seasonally fluctuating, hydrology (Tedesco et al. 2008, Mims and Olden 2012). In contrast, opportunistic species are small, exhibit fast growth, and have early sexual maturation (Winemiller 2005), all of which are advantageous in occupying systems with harsh and unstable hydrology

(Olden and Kennard 2010). However, modes of reproduction, specifically the nature of guarding behavior, placement of eggs within or on substrates, the ability to have multiple spawning bouts, and the seasonal affiliation for spawning, are also related to natural hydrologic variation (Balon 1975, Winemiller 2005). For example, brood hiders bury eggs in the substrate for protection, either from predators or high-flow disturbances, whereas open substratum spawners broadcast their eggs over substrates in brief temporal windows to avoid short-term high flows (Craven et al. 2010). Seasonal extremities in hydrology also determine the onset and length of spawning, as well as recruitment periods (Bunn and Arthington 2002). While some aspects of reproductive strategies (e.g., extent of parental care) represent components of the life history groups, reproductive strategies may reveal important adaptations to hydrologic variation undetected by coarser life history strategies.

Presumably, if relationships between natural flow and biota exist, ecological responses to altered hydrology can be predicted. Thus, if natural variation in stream flows is responsible for shaping the life history strategies of fish (Bunn and Arthington 2002) and hence, functional diversity of communities (Poff and Allan 1995), then alterations to natural hydrologic patterns may pose conditions in which those resident species are maladapted, leading to a loss or replacement of species (Moyle and Mount 2007). Although quantitative relationships between natural hydrology and ecological patterns are commonly used to suggest the consequences of hydrologic alteration (Poff and Allan 1995, Pyron and Lauer 2004), they are rarely used to make quantitative predictions of ecological responses to hydrologic alteration (McManamay et al. 2013). In contrast, ecological responses to hydrologic alteration are typically measured empirically as correlative relationships (Poff et al. 2010, Poff and Zimmerman 2010). Indeed, much of our understanding of the importance of natural flows to stream ecosystems, and the need to protect them, may be based on biotic responses to altered, rather than natural, conditions. The limitation of relying on correlations between altered hydrology and ecology to determine the importance of natural flows is that altered ecological conditions may be influenced by other factors that accompany hydrologic alteration, such as changes in water quality (Olden and Naiman 2010). Unless confounding variables are accounted for in analyses, conclusions regarding the importance of natural flows, and the cause of ecological changes, may be spurious. Alternatively, a proper understanding of how natural hydrology structures ecological communities may be required prior to predicting the ecological consequences to uncertain future scenarios (e.g., climate change; Tonn 1990).

Our first objective was to determine the role of hydrology in structuring continental patterns in fish assemblages using a trait-based approach. We chose to

evaluate continental patterns in fish traits because this reflects the role of hydrology in shaping the selective pressures influencing regional pools of species. In addition, the continental scale provides a foundation for assessing how major losses in natural flow variation may induce shifts in trait frequencies among regions. Poff et al. (2007) suggested that ubiquitous dam regulation, in conjunction with consistent hydrologic responses to dam regulation, leads to a homogenization of stream flow variation, i.e., loss in regionally distinct hydrology. In the same issue, Moyle and Mount (2007) further proposed that the uniformity of hydrology in river systems, species loss, and associated colonization by habitat generalists, has led to a homogenization of regionally distinct fish assemblages. Thus, these studies provided a framework for developing our second objective, i.e., to determine whether natural hydrology-trait models can be used to predict fish trait responses to altered hydrology. We hypothesized that if natural flow variation plays a role in structuring continental patterns in fish traits, then consistent losses in the uniqueness of natural flows may show predictable responses in fish communities.

METHODS

Developing fish trait frequency maps

Fish trait frequency (FTF) maps characterize the frequency or proportion of traits represented by fish assemblages within basins (Mims et al. 2010). FTF maps provide a means to examine how environmental variables, such as hydrology, structure fish assemblages across the landscape. However, assessing environmental-trait relationships requires accounting for phylogeny since species of similar phylogenetic lineage share characteristics and constraints through common evolutionary descent (i.e., phylogenetic inertia; Felsenstein 1985, Diniz-Filho et al. 1998). Controlling for phylogeny ensures patterns in traits across the landscape are attributable to environmental variation and not confounded by common lineage of species pools.

Geographic distributions (i.e., ranges developed from known presences) of 865 freshwater fish species within 2068 subbasins (eight-digit hydrologic catalog units [HUC8]) were available through NatureServe (NatureServe 2004). Lists of all native freshwater fish species, excluding estuarine fish, were compiled within each HUC8. Information on species life history requirements and reproductive strategies were accessed through the FishTraits database, which contains trait-related information for 810 species of freshwater fish (Frimpong and Angermeier 2009). Trait information for some species listed within NatureServe was incomplete due to insufficient biological information, being highly endemic and not formally described, or differences in nomenclature. For fish species without representative or complete trait information, we used NatureServe Explorer, FishBase (Froese and Pauly 2013), and literature searches to update missing traits with new information or find the

closest phylogenetic relative as a substitute. The closest phylogenetic relative was determined as the closest clade or parental clade (subgenus), species of potential hybridization, or species commonly misidentified as the species of interest (in that order of preference).

We obtained traits that could be used to summarize life history strategies or reproductive strategies. Life history traits included maximum length, age at maturation, longevity, and fecundity. Reproductive characteristics included spawning season timing, season length, and whether fish had more than one spawning bout. Mode of reproduction (sensu Balon 1975), represented as binary variables, ranged from absence of parental care (open substratum broadcast spawning) to placing eggs in specific substrates (brood hiders) to constructing nests and guarding young (substrate choosers and nest guarders) and bearing live young (bearers). Using similar methods as Winemiller and Rose (1992), we calculated parental care indices as indicative of the degree of parental investment ranging from 0 to 3: 0 for no parental care, 1 for specific placement of eggs, 2 for guarding eggs, and 3 for bearing young. Spawning timing was represented as the proportion of each month (January–December) falling within each species spawning season. The sum of all monthly proportions approximates the length of the spawning season. We calculated spawning season timing indices by summing the proportions falling into different seasonal windows: winter (December–February), spring (March–May), summer (June–August), and fall (September–November). Serial spawners, species having more than one spawning bout, were represented as binary variables. Nelson (2006) developed a family number (also available in FishTraits), which serves as a phylogenetic position of each family relative to other families (Frimpong and Angermeier 2009). Smaller family numbers represent more primitive fishes. Thus, to account for the effect of phylogenetic inertia on all traits, we used generalized linear models to predict fish traits from family number based on Gaussian, Poisson, and binomial distributions as appropriate. Using predicted values, we calculated deviance residuals for all variables to use in future analyses.

Freshwater fish life histories are represented as three major endpoints in the continuum of trade-offs among juvenile survival/parental care, fecundity, body size, and longevity (Winemiller and Rose 1992). The endpoints can be used as the basis for creating three life history groups, which include periodic, equilibrium, and opportunistic fish species (Winemiller and Rose 1992). Periodic species are larger-bodied fish characterized by late maturation, high fecundity, and low parental investment. Equilibrium species are smaller-bodied fishes with lower fecundity, but invest more in their progeny (i.e., provide more parental care), and hence, have high juvenile survival. Opportunistic fishes are typically small-bodied fish with early maturation, no parental investment, and extended spawning seasons

with multiple bouts. We hard assigned all fish species to one of three life history groups by determining the minimum Euclidean distance between each species multivariate trait position (seven traits) and each life history group's endpoint in trait space (Mims et al. 2010, Olden and Kennard 2010). For simplicity, we preferred the hard classification method over the soft classification approach, i.e., providing a distance measure from each species multivariate position to each endpoint (Mims and Olden 2013).

The periodic strategy endpoint represented maximum values for total length, age at maturation, longevity, and fecundity, and minimum values for serial spawning, season length, and parental care. The opportunistic strategy was characterized by maximum values for serial spawning and season length and minimum values for all other traits. The equilibrium endpoint had average values for longevity, maximum values for parental care and age at maturation, and minimum values for all other traits. Principal components analysis (PCA) on correlations among the seven traits was used to examine whether multivariate patterns represented by the species in our analysis resembled the three-endpoint life history continuum presented by Winemiller and Rose (1992). All variables were $\log(x + 1)$ transformed, centered to zero, and scaled to unit variance prior to analysis. Species were plotted according to their life history group along the first two principle components (PCs; see Appendix A).

Trait information was summarized separately for all fish species and only fish species preferring lotic environments. Although lotic specialists are presumed to be more adapted to hydrologic variation than lentic species, fish preferring lentic environments may be lotic dependent or influenced by hydrology. For example, bluespotted sunfish (*Enneacanthus gloriosus*) inhabit oxbows, backwaters, and wetlands in the coastal plain of the southeastern United States, and hence, they are typically defined as preferring lentic environments (Page and Burr 1991). However, bluespotted sunfish are highly dependent upon flood magnitude and duration to inundate floodplain wetlands (Lietman et al. 1991, Light et al. 1998). Because distinguishing the influence of hydrology based on lotic preference is difficult, we evaluated trait responses from all fish and only fish preferring lotic habitats (from here on, lotic fish). For life history traits, we summarized the proportion of species as periodic, equilibrium, or opportunistic within each HUC8 (e.g., Fig. 1). All other traits were summarized as the average deviance value across all species within each HUC8 (e.g., Fig. 1).

Assembling a hydrologic and landscape predictor data set

Our first objective was to determine the relative role of hydrologic variation in structuring fish assemblages; however, many nonhydrologic environmental variables are also potentially important. In addition, hydrology is highly interrelated with landscape variables; hence, we

constructed models predicting fish traits with hydrology and landscape variables independently and then combined. We assembled landscape predictors that summarized variation in geology, topography, climate, land cover, and primary productivity within each of 2068 HUC8 subbasins (Fig. 2). All variables and their sources are listed in Tables 1 and 2. Justification and methods for including landscape predictors are provided in Appendix B. All geospatial summarization procedures were conducted in ESRI ArcGIS 9.3.

Hydrologic variables were assembled using a three-step procedure: (1) isolating reference-quality stream gages across the United States (or gages with records extending prior to disturbance), (2) calculating summary hydrologic statistics from discharge records, and (3) summarizing hydrologic information across HUC8 subbasins. Reference-quality U.S. Geologic Survey (USGS) stream gages were considered streams with little or no hydrologic disturbance in their upstream watershed. We determined reference-quality criteria using documented lists of reference-quality stream gages (data *available online*),⁴ remarks within USGS annual water data reports (ADRs), visual examination of stream flow patterns (Vogl and Lopes 2009), and a GIS-based hydrologic disturbance index (HDI; see Falcone et al. [2010b]). The HDI represents the cumulative disturbance of dam regulation, channel modification, withdrawals, and landscape fragmentation (Falcone et al. 2010a). Gages with HDI <14 and with at least a 15-year complete hydrologic record were selected (gages with >5 days of missing values were excluded). HDI values of 14 were well within the range found in reference-quality gages (Falcone et al. 2010a). Based on ADR reports, we further excluded gages with reports mentioning regulation by dams, major diversions, channelization, and agriculture. Visual examination of hydrographs was used to identify apparent changes in stream flow patterns attributable to different anthropogenic stressors (Vogl and Lopes 2009). Stream gages with long hydrologic records extending prior to disturbance, such as dam regulation, also provide a source of reference-quality hydrologic information. We selected streams with pre-dam-regulation hydrologic records using a combination of information from ADR reports, National Inventory of Dams (NID; *available online*),⁵ information on disturbances upstream of each gage (Falcone et al. 2010b), and historical patterns in land and water use (McManamay et al. 2012a). We ensured pre-dam hydrologic records were not influenced by cumulative regulation by smaller dams and by other disturbances, such as urbanization or water use. Our final data sets resulted in 2618 stream gages with reference-quality hydrology data (see McManamay et al. [2014]).

⁴ http://water.usgs.gov/GIS/metadata/usgswrd/XML/gagesII_Sept2011.xml#Identification_Information

⁵ <http://geo.usace.army.mil/pgis/f?p=397:12>

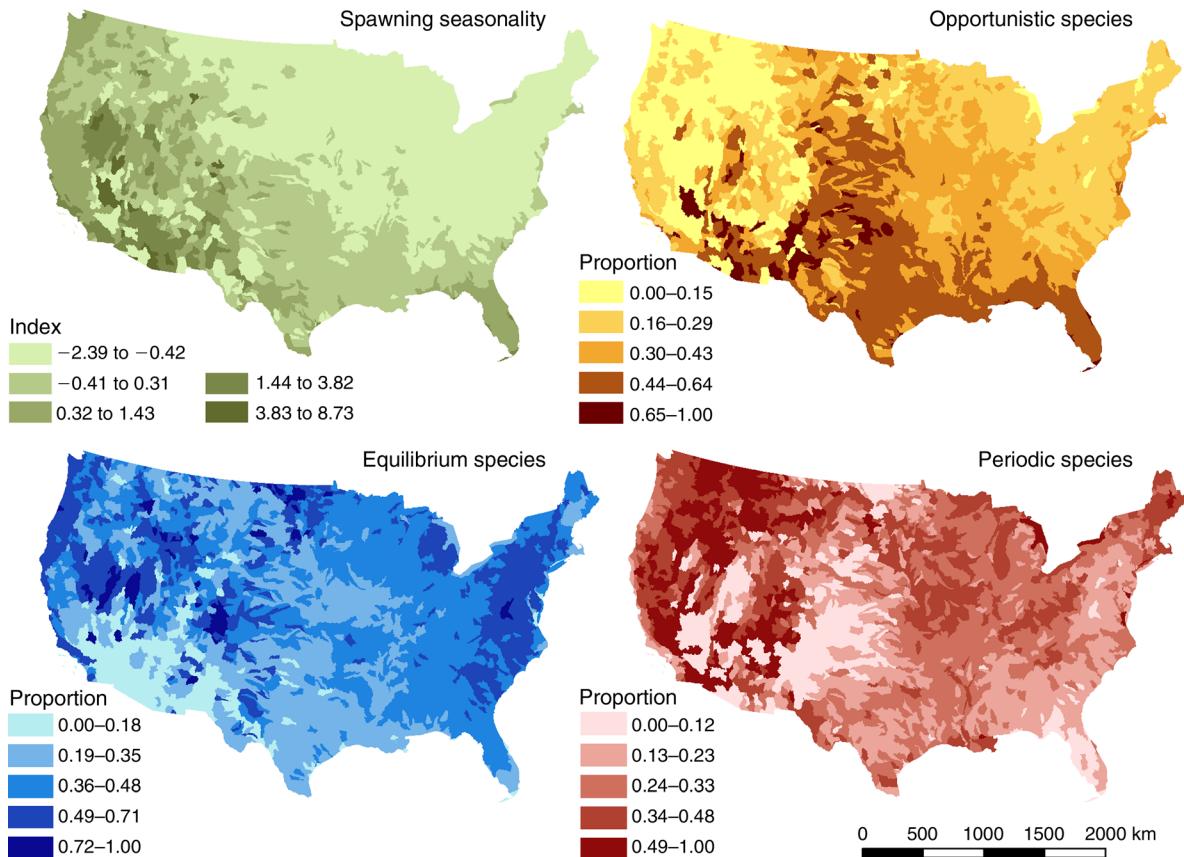


FIG. 1. Examples of fish trait frequency maps across the United States. Spawning seasonality is an example of a reproductive trait/strategy whereas equilibrium, opportunistic, and periodic species are examples of life history groups.

After compiling discharge records, we calculated 38 hydrologic statistics using the USGS hydrologic index tool (HIT; see Henriksen et al. [2006]), which included the 33 indicators of hydrologic alteration (Richter et al. 1996) and five additional variables important to describing ecological patterns (Richter et al. 1996, 1997, Olden and Poff 2003; Table 1). All magnitude-related hydrologic indices were divided by mean daily flow to standardize variables to ensure patterns in hydrology were due to spatial variation and not river size (Kennard et al. 2010). We then created Thiessen polygons (proximity tool set) using stream gage point locations (latitude and longitude). Hydrologic statistics were then summarized within HUC8 subbasins based on area-weighted averages of polygon overlap with watershed boundaries (Fig. 2).

Building hydrologic-trait models

Collinearity among trait frequencies, hydrologic predictors, and landscape predictors were examined using Spearman's rank correlations. Predictor variables with Spearman's rho values >0.80 were excluded in favor of variables that had more documented importance in predicting ecological patterns. We were conservative in removing correlated predictor variables

from the data set because subsequent analyses were robust against cases of multicollinearity.

In order to determine the relative contribution of hydrology in explaining fish trait frequencies, we used redundancy analysis (RDA) to examine partial variation between hydrology, landscape variables, and their combined effect. RDA provides a mechanism to determine the amount of unique variation in multiple response variables attributable to multiple explanatory variables or multiple sets of explanatory variables (McCune and Grace 2002). Partial variance was calculated for hydrology and landscape variables using the varpart function in the vegan package in the R programming environment (Oksanen et al. 2013). Each independent variable data set was conditioned upon the other to determine unique variation attributable to hydrologic or landscape variables. We conducted RDAs to explain variation in reproductive strategies and life history groups under six scenarios: predicting all fish using all predictors, only hydrologic predictors, and only landscape predictors, and predicting lotic fish using all predictors, only hydrologic predictors, and only landscape predictors.

While RDA provides an approach to assess partial variance, it does not provide quantitative predictions of

hydrology-trait relationships. Random forests were developed in R and used to predict fish trait values based on hydrologic and landscape predictors in the six scenarios mentioned above. Random forests are an improved form of exploratory learning over traditional tree-based approaches, in that they have increased classification accuracy and advanced approaches to estimating variable importance (Brieman, 2001, Cutler et al. 2007). Random forests improve accuracy by generating a large number of classification trees (typically 500) and then combining the predictions from all trees. Each tree is generated from a random subset of variables and a bootstrap subsample of the data (63% of observations). The remaining samples (out of bag [OOB] observations) are used in a cross-validation procedure to calculate the percentage of variance explained (%Var), mean-squared error (MSE), and variable importance. Model performance was assessed using percentage of variance explained across all six scenarios for all traits. Combined effects (%Var_{CE}) of hydrology and landscape variables in random forest models were calculated using

$$\%Var_{CE} = (\%Var_{HYD} + \%Var_{LAND}) - \%Var_{ALL} \quad (1)$$

where HYD, LAND, and ALL refers to percentage of variance explained by each individual data set, hydrologic, landscape, and the two combined, respectively.

To calculate variable importance, values of each variable for OOB observations are randomly permuted and then predicted using each tree. Variable importance was assessed using the proportional increase in MSE values (IncMSE), which is calculated as the average increase in MSE with the absence of each predictor in randomly permuted OOB data. In order to compare the importance of predictors across models, we standardized IncMSE values by the maximum value for each model to compute relative value (Rel-IncMSE). We then calculated mean Rel-IncMSE as averages across all-variable models to ascertain the relative importance of hydrology vs. landscape predictors in structuring patterns in traits.

Predicting fish trait responses to hydrologic alteration

The advantage of models predicting trait–natural-hydrology relationships is that they can then be applied to predict ecological consequences of hydrologic alteration, such as that induced by dam regulation. Of the 2618 reference-quality gages used to construct hydrologic-trait models, 233 had at least 15 years of pre- and post-dam-regulation information (Fig. 3; McManamay et al. 2014). We ensured these gages had no evidence of disturbances induced by other factors besides dam regulation (McManamay et al. 2014). The same 38 hydrologic statistics mentioned in *Methods: Assembling a hydrologic and landscape predictor data set* were calculated for pre- and post-dam-regulation hydrologic records. All magnitude-related variables were standardized by dividing by mean daily flow. To explore the multivariate hydrologic response of streams to dam

regulation, we conducted a principal components analysis (PCA) on the 38 hydrologic statistics from pre- and post-hydrologic records. We plotted the first three significant principal components (PCs) to examine multidimensional patterns (significance based on broken stick method; Jackson [1993]). Combinations of variables with the highest loadings along the significant PCs were selected by sorting loadings and then using breaks in the distribution to select the most influential variables. Percent changes from pre to post-dam-regulation were visually examined using a subset of variables with highest loadings.

Hydrologic-trait models (developed previously) were used to predict trait responses for pre- and post-dam regulation for four of the six scenarios mentioned previously (only models containing hydrologic predictors). To isolate the effects of hydrology, the pre- and postvalues for the 38 hydrologic variables were changed while landscape predictors were kept constant. Landscape predictors were represented by the HUC8 in which each dam regulated gage was located. Trait-frequency responses were represented as the percentage of changes from predam conditions. Because negative deviance values would result in inappropriate calculations of the percentage of changes, we shifted all traits frequencies on a scale >0 while keeping differences in relative magnitudes the same. Differences between trait frequencies from pre- to post-dam regulation were tested for significance using Kruskal-Wallis tests, whereas differences for all reproductive and life history traits among pre- and postscenarios were simultaneously tested for significance using a permutational multivariate analysis of variance (PMANOVA) in the vegan package in R (Stevens and Okasanen 2012). PMANOVA is analogous to a nonparametric MANOVA but uses distance matrices to partition sum of squares and then calculates pseudo F statistics following using large permutations (we used 500).

Because geographic, hydrologic, and operational (i.e., dam purpose) context may structure the effects of hydrologic alteration, we hypothesized that classification systems may explain variation in trait-frequency responses to dam regulation. Provinces, ecoregions, and hydrologic classifications have been identified as important frameworks for stratifying hydrologic analyses (Johnson and Fecko 2008, McManamay et al. 2012a) and fish communities (Wolock et al. 2004, Frimpong and Angermeier 2010a). Classifying dams by their operational purpose can also provide a template to evaluate hydrologic and ecological responses to dam regulation (Poff and Hart 2002). Provinces, ecoregions, and hydrologic classes were assigned to each dam-regulated gage based on the dominant region within each HUC8. Using information from the NID and ADR reports, we developed five simplified categories of purposes hypothesized to have varying effects on hydrology, and thus ecology: diversion, other (recreation, farm ponds), water supply, flood control (includes

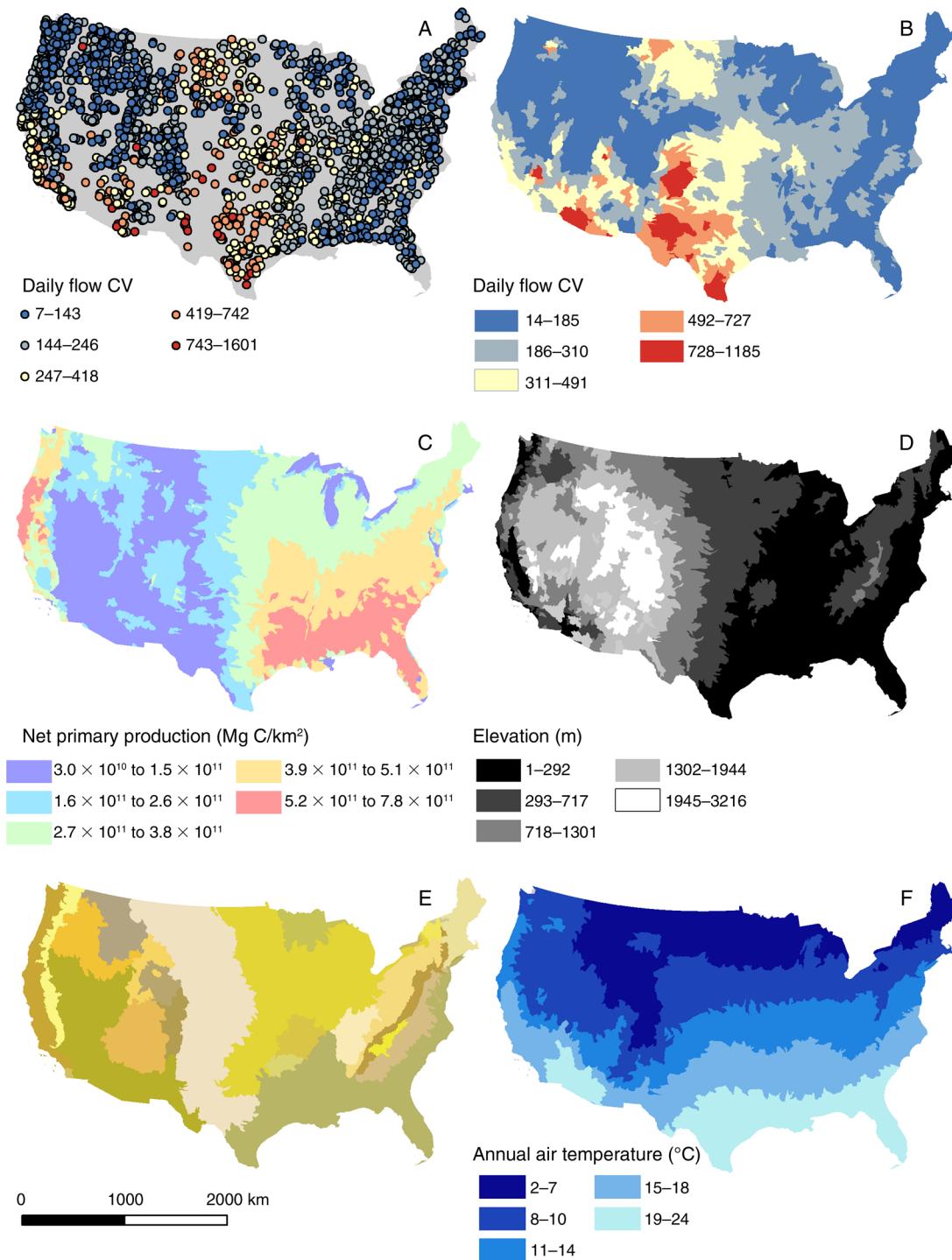


FIG. 2. Examples of (A, B) hydrologic and (C, D, E, F) landscape predictors. (A) Using hydrologic statistics from USGS stream gages, hydrologic variables were summarized in (B) HUC08 subbasins. The key for physiographic provinces in panel (E) is provided in Appendix B.

navigation), flood control + water supply, hydropower, and hydropower + additional purposes. All classifications were compared in their ability to explain variation in hydrologic and trait-frequency responses using

PMANOVAs for all four scenarios (for more information, see Appendix D).

Organizing our analysis by geographic regions also provides a method to examine whether regionally

TABLE 1. Hydrologic predictors used in fish trait models.

Variables	Description
Magnitude	
MA3	daily coefficient of variation in flow
MA12–MA23	mean monthly flows (January–December)
MA41	mean annual runoff
ML17	baseflow index
MH20	annual maximum
Duration	
DL1–DL5†	various duration low flows (1, 3, 7, 30, 90 day)
DL16	low flow duration
DL18	zero-flow days
DH1–DH5†	various duration high flows (1, 3, 7, 30, 90 day)
DH15	High-flow duration
Frequency	
FL1	low-flow frequency
FH1	high-flow frequency1
FH6	high-flow frequency2
FH7†	high-flow frequency3
Timing	
TA2	predictability in flows
TL1	day of year of annual minimum‡
TH1	day of year of annual maximum‡
Rate of change	
RA1	rise rate
RA3	fall rate
RA8	reversals

Note: Source is Olden and Poff (2003).

† DL2, DL4, DH2, and DH4 were removed due to being correlated with other low-flow (DL) and high-flow (DH) metrics. FH7 was removed due to being correlated with FH6.

‡ Day of year with 1 January = 1.

distinct hydrology and trait frequencies become less distinct or homogenized following dam regulation, as suggested by Poff et al. (2007) and Moyle and Mount (2007). We used analysis of similarities (ANOSIM) in the vegan package in R to test whether hydrology and trait frequencies were less distinct following dam regulation. ANOSIM tests for significant differences by comparing rank dissimilarities between geographic regions to within geographic regions. The ANOSIM statistic R is calculated based on the difference in mean ranks between groups (r_B) and within groups (r_W) using $R = (r_B - r_W)/(N(N - 1)/4)$. R ranges from -1 to $+1$ where a value of 0 indicates complete random grouping, values of $+1$ indicate high dissimilarity between groups, and values of -1 indicate high dissimilarity within groups. We hypothesized that if dams were homogenizing hydrology and trait frequencies, dissimilarities among geographic regions would be higher (higher R values) during pre-dam compared to post-dam conditions. ANOSIM was used to analyze dissimilarities in pre- and posthydrology and pre- and posttrait frequencies among provinces, ecoregions, and hydrologic classes for all four scenarios.

RESULTS

Fish trait frequency maps

Overall, we assembled trait information for 850 native freshwater fish species in the conterminous United States. Family number was significantly related to fish traits in all generalized linear models except those for serial spawners and brood hidiers. Using Winemiller and Rose's (1992) life history groups, we identified 141 species as periodic strategists, 351 as opportunistic strategists, and 358 as equilibrium strategists. Multivariate patterns in species' life history strategies represented the three-endpoint life history continuum presented by Winemiller and Rose (1992; see Appendix A). Although fish trait frequency maps suggested there was some regionality in trait frequencies, maps also suggested geographically separated areas shared similar values (Fig. 1). The majority of fish were classified as lotic (757) compared to lentic (110) species. Most trait values were similar among lotic and lentic species; however, lentic species had higher values for season length and nest guarding, but lower values for substrate choosers (Appendix A). A higher proportion of periodic species and lower proportion of equilibrium species were represented within lentic species compared to lotic species.

Hydrologic and landscape predictors

Relationships were evident among landscape predictors, among hydrologic predictors, and between landscape and hydrologic predictors (Appendix B). For example, PMPE (mean precipitation–potential evapotranspiration [PET]) was positively correlated to mean annual runoff and negatively correlated with DL18 (zero flow days; Appendix B). Physiographic provinces differed markedly in their ranges in mean annual runoff values. Because of the redundancy in information, PMPE, PET, relief, minimum and maximum precipitation, percent forest land cover, and minimum and maximum temperature were removed from the landscape variables. Likewise, the following hydrologic variables were removed from the predictor data set: DL2, DL4, DH2, DH4, and FH7 (see Table 1 for definitions of variables).

In general, correlations among trait frequencies were weak, especially between reproductive strategies and life history groups (Appendix B). However, a strong positive correlation was observed between opportunists and serial spawners and between opportunists and summer spawners. Winter and fall spawners were positively correlated with each other and season length. Brood hidiers were negatively correlated with serial spawners. Correlations between predictors and fish traits were also observed; however, considerable unexplained variation was evident in fish traits when examined using univariate relationships. Brood hidiers were positively correlated, whereas nest guarders were negatively correlated with slope. Summer spawners were positively correlated with

TABLE 2. Landscape predictors used to build fish trait models.

Variable	Description	Source
Geology		
PHYS	physiographic provinces	Fenneman and Johnson (1946)
BDRKPERM	bedrock permeability class (1–7)	Wolock et al. (2004)
SAND	percent sand	Wolock et al. (2004)
Topography		
ELEV	elevation (m)	Hastings et al. (1999)
RELIEF†	relief (maximum–minimum elevation)	Hastings et al. (1999)
SLOPE	mean slope (%)	Wolock et al. (2004)
PFLATT†	percentage of land that is flat (<1% slope)	Wolock et al. (2004)
Climate		
MEANPREC	30-year mean precipitation	PRISM (2013)
MINPREC†	30-year minimum precipitation	PRISM (2013)
MAXPREC†	30-year maximum precipitation	PRISM (2013)
MEANTEMP	30-year mean air temperature	PRISM (2013)
MINTEMP†	30-year minimum air temperature	PRISM (2013)
MAXTEMP†	30-year maximum air temperature	PRISM (2013)
PET†	potential evapotranspiration	Wolock et al. (2004)
PMPE†	MEANPREC-PET	Wolock et al. (2004)
Land cover		
FOREST†	percent forested (41–43)	MRLC (2013)
DEVELOP	percent developed (21–24)	MRLC (2013)
AGRICUL	percent agriculture (81, 82)	MRLC (2013)
OPENH2O	percent open water (11)	MRLC (2013)
ICESNOW	percent ice and snow (12)	MRLC (2013)
BARREN	percent barren (31)	MRLC (2013)
WETLAND	percent wetland (90, 95)	MRLC (2013)
SCRUB	percent scrub/shrub (51–52)	MRLC (2013)
GRASS	percent grassland/herbaceous (71)	MRLC (2013)
Other		
NPP	net primary production	Imhoff et al. (2004)

Note: Numbers in parenthesis that follow description represent codes for different land covers from the National Land Cover Dataset.

† Indicates variable was removed due to correlation with other variables.

mean temperature. Opportunists were positively correlated with daily flow CV (coefficient of variation in flow), whereas equilibrium species were negatively correlated. Opportunists were also positively correlated with 1-day high flow and rise rate.

Hydrologic trait models

Based on the redundancy analysis, hydrologic and landscape variables shared considerable overlap in explaining variation in trait frequencies (Table 3; Appendix B). Hydrologic variables explained 42% of total variation in reproductive strategies (for all fish and only lotic fish), slightly higher than variation attributed to landscape variables (40–41%, adjusted R^2 ; Table 3). After conditioning variables, hydrology and landscape variables explained 11% and 10%, respectively, of the partial variance in reproductive strategies. Hydrologic variables explained less of the total variance and partial variance in life history groups (30–33% and 6–7%, respectively) compared to landscape variables (37–39% and 13%, respectively). Total variance explained by combined effects was higher than that of hydrology or landscape variables when considered separately, but the difference was more apparent when considering partitioned variance (Table 3).

With the exception of models predicting open substratum and fall spawner indices, random forest models including all fish explained more variation in traits and had lower MSE than models including only lotic fish (Table 4). Random forests predicting winter spawners had the highest predictive capacity, whereas models predicting bearers had the lowest. Models including all variables or only landscape variables explained more variation and had lower MSE than models including only hydrologic variables; however, the performance of hydrologic variable models was comparable to other models. In addition, the variance explained by the combined effect between landscape and hydrologic variables was high and in many cases composed the majority of variation in fish traits (Table 4).

Variables with the highest importance in the all-variable models excluded hydrologic predictors (Appendix C). Physiographic province, mean temperature, slope, and elevation had the highest Rel-IncMSE values. Rel-IncMSE is the relative (or standardized) increase in mean squared error. Among the hydrologic variables, seven-day and one-day duration high-flows, annual runoff, the Julian date of annual maximum, and various monthly magnitude flows had among the highest Rel-

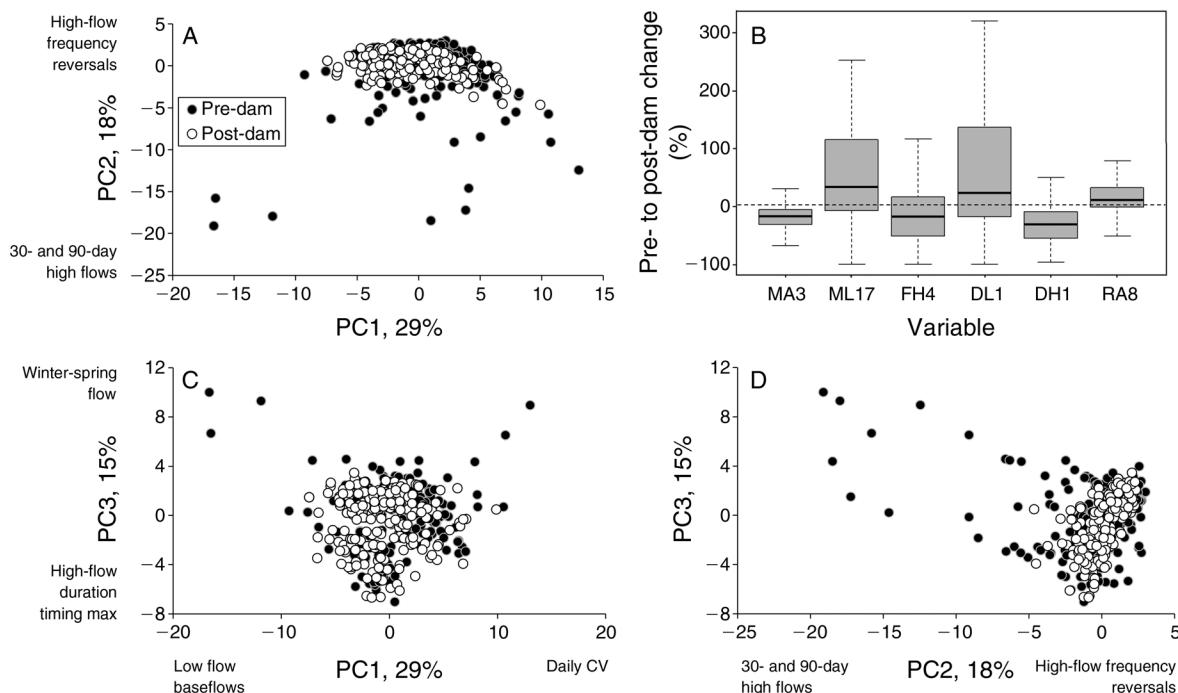


FIG. 3. Ordination of USGS stream gages using their pre- and post-dam-construction hydrologic statistics in principal components analysis (PCA). Scores for the first three significant PCs were plotted. Variables along each PC axis represent statistics with the highest loadings along PCs. (B) Box plot of percentage of change in a subset of hydrologic statistics with highest loading values (variable names provided in Table 1). The center line is the median value. Box edges are the 25th and 75th percentiles, and whiskers represent the 5th and 95th percentiles.

IncMSE values. Models constructed using only hydrologic variables displayed similar patterns in variable importance. In contrast to the model including all variables, models constructed with only hydrologic variables had Rel-IncMSE values displaying more of a gradual decline from hydrologic variables with the highest importance to lowest importance.

Predicting fish trait responses to hydrologic alteration

The 233 stream gages with pre- and post-dam-regulation information had widespread distribution across the United States. According to the broken stick method, the first five principal components were significant and explained 77% of the total variation. PCA consistently showed that pre-dam regulation occupied a larger multivariate space than post-dam-regulated records (Fig. 3). Dam regulation generally increased baseflows, low flows, and reversals but decreased maximum flows, high-flow frequency, and daily flow variation (Fig. 3). Longer duration high flows (30- and 90-day flows) tended to increase with post-dam regulation.

When considering all-variable models for all fish, predicted trait responses to dam regulation were not significantly different between pre- and post-dam scenarios for reproductive strategies (PMANOVA, $F_{1,470} = 0.188$, $P = 0.862$) or life history groups (PMANOVA, $F_{1,470} = 1.01$, $P = 0.359$). Likewise, trait

responses to dam regulation for the all-variable lotic-fish model were not significant for reproductive strategies (PMANOVA, $F_{1,470} = 0.192$, $P = 0.844$) or life history groups (PMANOVA, $F_{1,470} = 1.242$, $P = 0.275$). For individual traits, the majority of responses to dam regulation were not significant with the exception of substrate choosers displaying significant increases (Kruskal-Wallis, $P < 0.05$) and bearers displaying significant decreases for lotic fish only (Kruskal-Wallis, $P = 0.05$).

In contrast to all-variables models, models using only hydrologic variables displayed significant changes for all-fish and lotic-fish scenarios (PMANOVA): all fish reproductive ($F_{1,470} = 3.10$, $P = 0.046$), all fish life history ($F_{1,470} = 3.95$, $P = 0.030$), lotic fish reproductive ($F_{1,470} = 3.60$, $P = 0.036$), and lotic fish life history ($F_{1,470} = 8.22$, $P = 0.004$; see Fig. 4). Spawning season, substrate choosers, brood hidiers, and winter/fall spawners all displayed significant increases whereas bearers, open substratum spawners, and summer spawners all displayed significant decreases (Kruskal-Wallis, $P < 0.05$; see Fig. 4).

In all four scenarios, models predicted a slight shift toward the equilibrium endpoint (Figs. 4, 5). Equilibrium strategists displayed consistent increases, whereas periodic and opportunistic strategists displayed decreases (Figs. 4, 5); however, responses were only significant for equilibrium strategists in the hydrologic variable

TABLE 3. Proportion of total variance (R^2 adj.) and partial variance in fish-trait frequencies explained by hydrologic predictors, landscape predictors, and their combined effect (taken from redundancy analysis).

Response	Hydrology		Landscape		Combined	
	R^2 adj.	Partial variance	R^2 adj.	Partial variance	R^2 adj.	Partial variance
All fish						
Reproductive	0.42	0.11	0.41	0.10	0.53	0.31
Life history	0.33	0.07	0.39	0.13	0.46	0.13
Lotic fish						
Reproductive	0.42	0.11	0.40	0.10	0.52	0.31
Life history	0.30	0.06	0.37	0.13	0.43	0.24

Notes: Analyses were conducted separately for all fish and for only lotic preferring fishes and for reproductive strategies and life history strategies. R^2 adj. stands for the adjusted R^2 value.

models for all fish and lotic fish (Kruskal-Wallis, $P = 0.002$ and $P < 0.0001$, respectively). Fish assemblages showed more variation and occupied a larger trivariate life history space for the all-variable models compared to the hydrologic models (Fig. 5).

Considerable geographic variation among responses suggested that ecohydrologic responses to dam regulation may be context specific (Fig. 6). For several traits, variation in trait responses seemed to follow an east to west pattern across physiographic provinces (Fig. 7A) and an intermittent to stable flow pattern across

hydrologic classes (Appendix D). Diversion dams, as opposed to other dam purposes, were predicted to favor species preferring intermittent-type environments (Fig. 7B). Hydropower and flood control dams have the largest predicted shifts in trait frequencies (Fig. 7B). Hydrologic responses to dam regulation were only significantly different among hydrologic classes (PMA-NOVA, $F_{12, 223} = 2.95$, $P = 0.020$) as opposed to provinces, ecoregions, and dam purpose (Appendix D). In general, hydrologic classes and provinces explained the most variation in trait responses across all scenarios;

TABLE 4. Comparison of performance among random forest models using various subsets of predictors (all predictors, landscape only, or hydrology only) in predicting variation in fish trait frequencies for all fish species or only those preferring lotic habitats.

Model	All		Landscape		Hydrology		Combined %Var
	%Var	MSE	%Var	MSE	%Var	MSE	
All fish							
Serial	62.3	0.05	61.5	0.05	55.6	0.1	54.8
Season	68.3	0.29	64.2	0.33	58.1	0.4	54.0
Bearer	21.3	0.01	32.3	0.01	18.5	0.01	29.6
Open substratum	46.7	0.07	47.7	0.06	33.1	0.08	34.0
Brood hider	65.1	0.04	63.3	0.04	56.8	0.05	54.9
Winter	72.4	0.05	68.9	0.06	63.3	0.07	59.8
Spring	53.9	0.04	53.1	0.04	46.0	0.05	45.1
Summer	65.6	0.06	66.7	0.06	54.6	0.08	55.7
Fall	58.6	0.05	58.9	0.05	47.0	0.06	47.3
Substrate chooser	53.4	0.01	53.2	0.01	42.1	0.01	42.0
Nest guarder	49.7	0.07	51.9	0.06	43.5	0.08	45.8
Periodic	52.1	0.01	53.5	0.01	36.9	0.01	38.3
Equilibrium	50.6	0.01	52.9	0.01	38.3	0.01	40.6
Opportunistic	66.0	0.01	65.8	0.01	57.5	0.01	57.3
Lotic fish only							
Serial	59.9	0.05	59.7	0.05	52.8	0.06	52.6
Season	65.2	0.35	61.3	0.39	55.5	0.45	51.7
Bearer	21.3	0.01	21.3	0.01	12.7	0.01	12.7
Open substratum	47.2	0.07	47.8	0.07	34.2	0.09	34.8
Brood hider	64.4	0.05	63.0	0.05	55.8	0.06	54.4
Winter	72.7	0.06	69.7	0.06	63.0	0.08	60.0
Spring	47.5	0.05	46.1	0.05	40.2	0.05	38.8
Summer	64.3	0.06	65.0	0.06	52.4	0.08	53.1
Fall	60.7	0.05	61.6	0.05	48.3	0.07	49.1
Substrate chooser	48.8	0.01	49.5	0.01	36.6	0.01	37.3
Nest guarder	48.3	0.07	50.1	0.07	42.0	0.08	43.8
Periodic	52.1	0.01	52.1	0.01	33.8	0.01	33.8
Equilibrium	50.6	0.01	50.6	0.01	37.1	0.02	37.1
Opportunistic	66.0	0.01	66.0	0.01	56.1	0.01	56.1

Notes: %Var and MSE refers to the percentage of variance explained and mean squared error, respectively, in the out of bag (OOB) sample. Combined effect refers to the amount of overlapping variation explained by landscape and hydrologic predictors. Numbers in bold refer to highest percentage of variance.

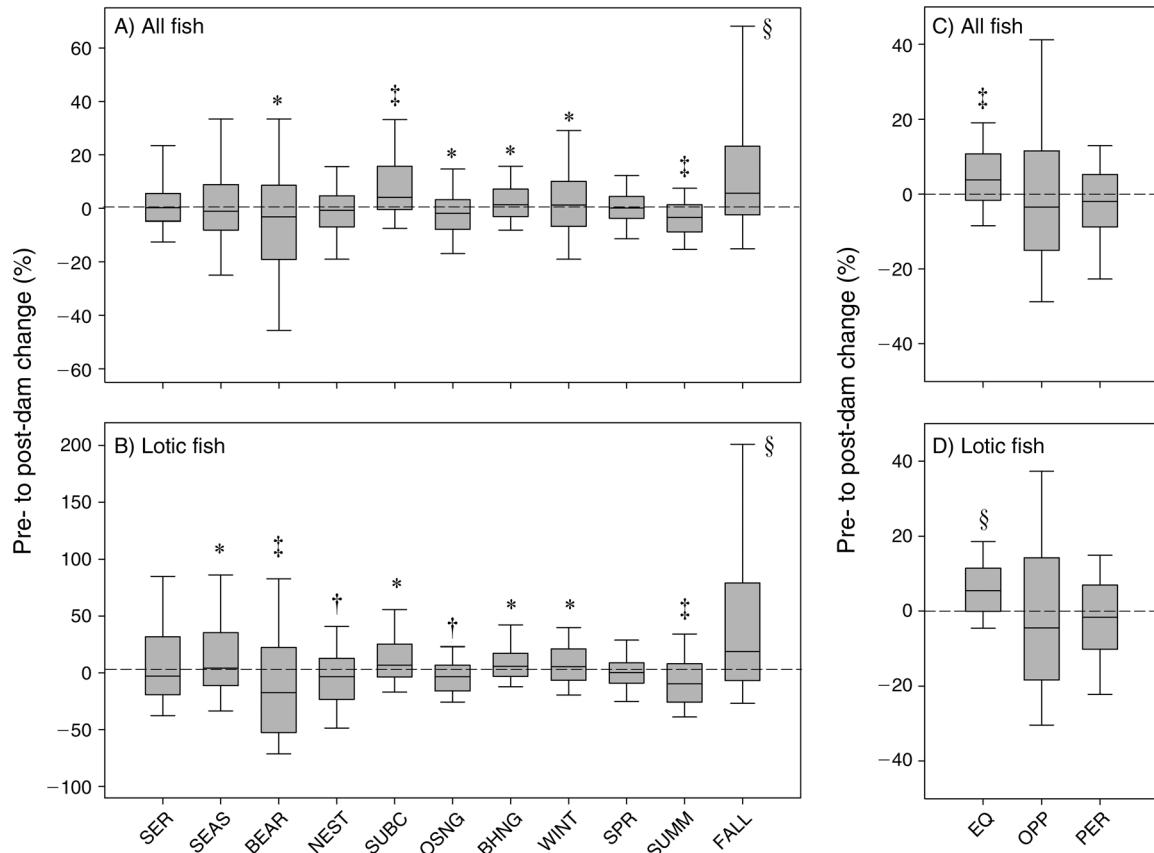


FIG. 4. Predicted percentage of changes in fish trait frequencies from pre- to post-dam regulation for (A, B) reproductive strategies and (C, D) life history groups using results from the hydrologic-variable model. Analyses were conducted separately for all fish and for lotic fish only. Key to abbreviations: WINT, winter; SPR, spring; SUMM, summer; FALL, fall; SER, serial spawners; SEAS, spawning season length; BEAR, bearers; NEST, nest guards; SUBC, substrate choosers; OSNG, open substratum nonguards; BHNG, brood hiders nonguards; EQ, equilibrium strategists; OPP, opportunistic strategists; and PER, periodic strategists.

† $P < 0.1$, * $P < 0.05$, ‡ $P < 0.005$, and § $P < 0.0005$, indicating significant differences between pre- and postregulation values for each trait using Kruskal-Wallis tests.

however, ecoregions explained the most variation in life history responses when predicted from the all-variable model. Reproductive strategies displayed significant changes among ecoregions and hydrologic classes for the all-variable model and among all three classification systems for the hydrologic variable models (PMANOVA, $P < 0.05$). Life history group responses were significantly different among hydrologic classes, provinces, and ecoregions for the all-variable and hydrologic variable scenarios (PMANOVA, $P < 0.05$; see Appendix D). Dam purpose explained the least amount of variance in all scenarios. All geographic classification systems explained more variation in trait responses when combined with dam purpose.

According to ANOSIM, hydrology displayed more regionally distinct patterns (higher R statistics) among hydrologic classes, provinces, and ecoregions during pre-dam regulation vs. post-dam regulation (Fig. 8). In the all-variable model for all fish, differences in ANOSIM R statistics between pre- and post-dam-

regulation conditions were minimal for both reproductive strategies and life history groups, with preregulation R values being lower than postvalues in some cases. For the hydrologic variable models for all fish, ANOSIM R statistics displayed consistent decreases from pre- to post-dam regulation for both reproductive strategies and life history groups (Fig. 8).

DISCUSSION

Our study reemphasizes that natural hydrologic variation does play a role at the continental scale in structuring fish assemblages. However, isolating the precise function of hydrology relative to landscape variables in shaping fish traits is extremely difficult since hydrology is interrelated with many abiotic factors. Nonetheless, the continuum of fish trait frequencies along hydrologic gradients in the landscape is evidence that natural hydrologic variation exerts selective pressures on regional fish species pools (Smith and Powell 1971, Tonn 1990, Mims et al. 2010). Because hydro-

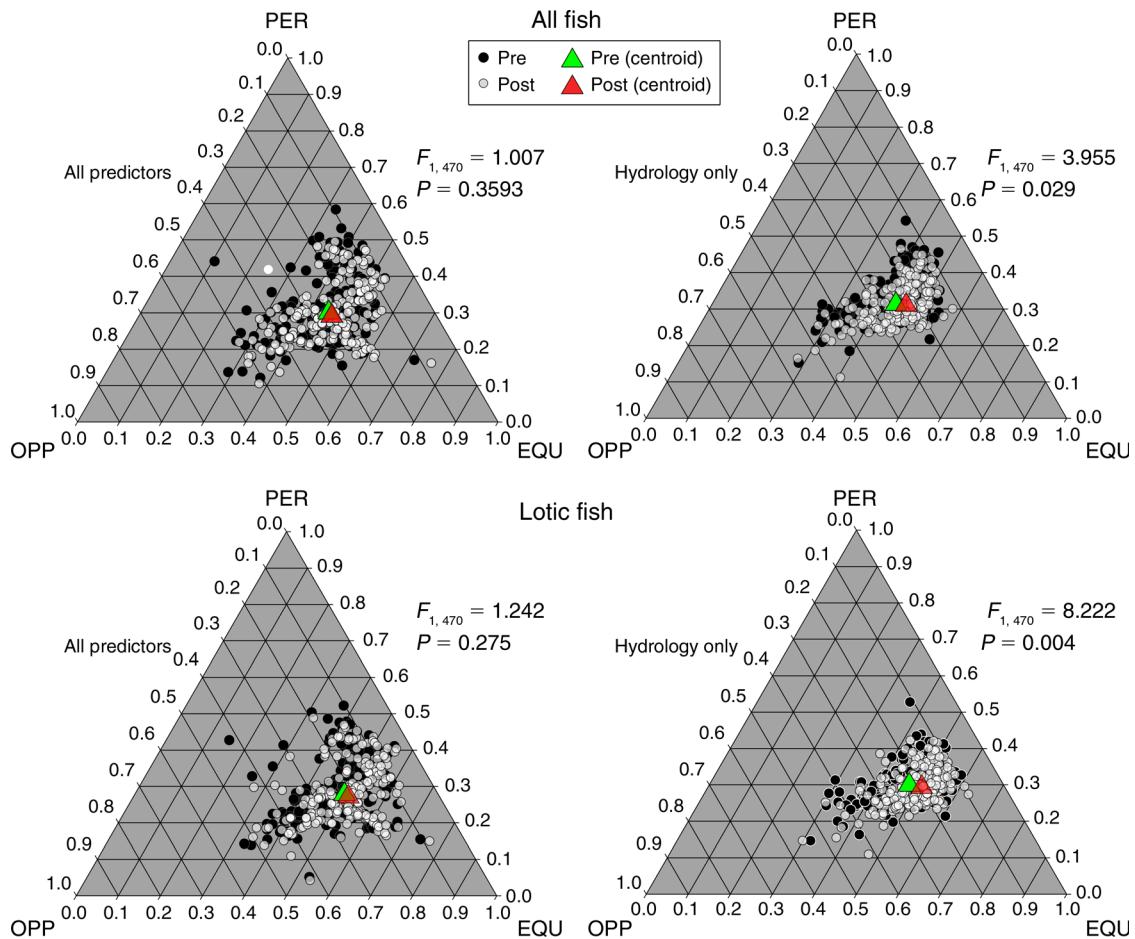


FIG. 5. Predicted shifts in the proportion of life history strategies from pre- to post-dam regulation using four scenarios. Four scenarios included analyses for all fish and for lotic fish only and predicting shifts using all variables vs. hydrologic variables only. Differences in the proportion of life history groups between pre- (PRE) and postregulation (POST) were tested for significance using a permutational multivariate analysis of variance. See Fig. 4 for definitions of abbreviations.

climatic conditions act as a filter in shaping the local species within basins (Jackson et al. 2001), it logically follows that widespread and consistent reductions in natural hydrologic variation should also exert selective pressures that are mirrored by changes in fish trait frequencies. Our results demonstrate that widespread reductions in natural flow variation due to dam regulation lead to an increased uniformity of fish life histories and reproductive strategies across the United States (Moyle and Mount 2007) with favored selection of the equilibrium strategy as found by others (e.g., Mims and Olden 2013) and favored selection of reproductive strategies with extended spawning seasons and preference for stable conditions, such as brood hidiers and substrate choosers.

Hydrologic filtering of fish traits across the United States

The fact that fish life history strategies vary regionally according to hydrologic selection pressures is not a new concept (Smith and Powell 1971, Tonn 1990, Mims et al. 2010). Similar to other studies, we observed trends that

suggested adaptations in life histories and reproductive strategies along hydrologic gradients (Mims et al. 2010, Olden and Kennard 2010). According to the tri-life history framework proposed by Winemiller and Rose (1992), opportunistic strategists have short life spans, low parental investment, and multiple spawning bouts a year. Thus, opportunistic fish inhabit harsher environments with unpredictable hydrology and recolonize rapidly following disturbances (Winemiller 2005). In contrast, equilibrium strategists have low fecundity and high parental investment, an artifact of inhabiting predictable, stable perennial flows (Winemiller 2005). In accordance with the exiting theory, we found that opportunistic strategists increased with increasing daily flow variation, whereas equilibrium species decreased. Similarly, Mims and Olden (2012) found that opportunistic strategists were positively related to flow variability, whereas the opposite was true for equilibrium strategists. Within selected basins of the United States and Australia, Olden and Kennard (2010) observed the same pattern with opportunistic species but not for

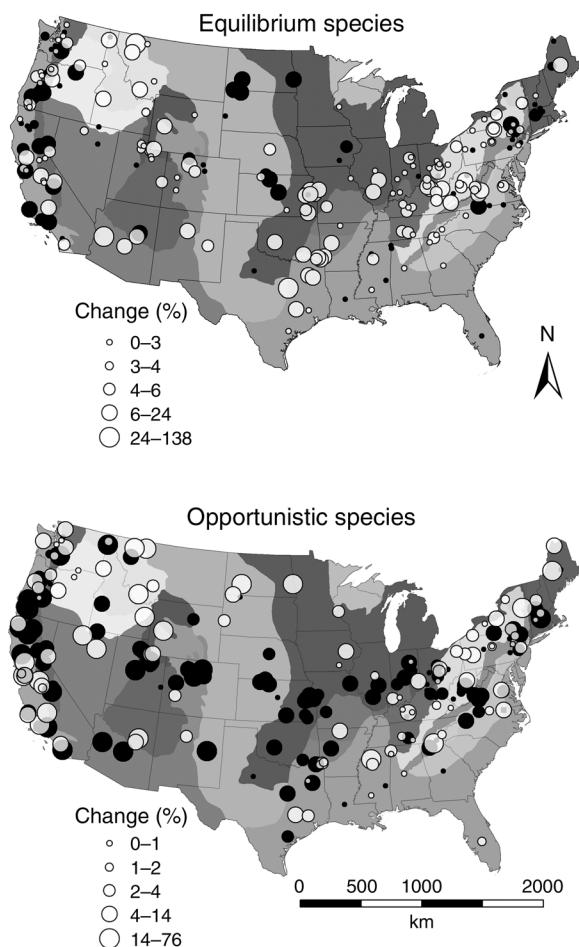


FIG. 6. Geographical variation in predicted positive (white dots) and negative (black dots) percentage of change in the proportion of life history strategies across physiographic provinces in the United States following dam regulation.

equilibrium species. Equilibrium strategists composed a higher proportion of species in basins with extended wet seasons and higher stability within the tropics of West Africa (Tedesco et al. 2008). Periodic strategists have adapted to seasonally fluctuating, but predictable hydrology by growing to large sizes, having late sexual maturation, and having high fecundity for successfully reproducing under suitable conditions. However, these strategies, along with low parental care, come at the expense of low juvenile survivorship and poor adaptive qualities to reproduce when conditions are seasonally unpredictable. Both Tedesco et al. (2008) and Mims and Olden (2012) reported that periodic strategists were associated with higher flow seasonality. In contrast, we did not observe any strong correlations for periodic species; however, this may have been the result of having no single hydrologic metric that summarized seasonality.

Compared to life history groups, adaptations of reproductive strategies to hydrologic variability have

received less attention (Craven et al. 2010, Carlisle et al. 2011). Serial spawners (e.g., *Cyprinella* spp.) have multiple spawning bouts within a season (Balon 1975). As would be expected, serial spawners were positively correlated with daily flow variation, short-duration high flows, and rapid rise/fall rates. In contrast, brood hidiers were negatively correlated to daily flow variation and short-duration high flows but positively correlated with annual runoff. As the name suggests, brood hidiers, such as brook trout (*Salvelinus fontinalis*), deposit eggs within the substrate but do not guard nests (Balon 1975); thus, these species prefer stable and predictable systems that prevent red dewatering or destruction. Although many reproductive traits mirror their respective tri-life history groups (e.g., serial spawners and opportunistic species), nest guarders do not mirror the equilibrium strategies in relation to flow. Given that nest-guarding fishes are representative of higher parental care, we presumed that nest guarders would be affiliated with stable environments similar to equilibrium strategists. However, opposite to equilibrium species, nest-guarding fishes were affiliated with unstable environments, i.e., positively correlated to short-duration high flows and daily flow variation. Nest-guarding behavior may be advantageous in unpredictable environments, since optimal nest habitat can be selected in areas protected from flashy high flows. We observed that many nest-guarding fishes display a bet-hedging strategy (Cole 1954, Olden and Kennard 2010) along the life history axis between the equilibrium and opportunistic endpoints. Olden and Kennard (2010) suggested Australian fishes characterized bet-hedging strategies by occupying a life history space along the axis connecting the opportunistic and periodic endpoints. When conditions are extremely harsh and recruitment completely fails, fish possess traits for rapid recolonization and reproduction (Olden and Kennard 2010). In contrast, nest-guarding fish in the United States, such as redear sunfish (*Lepomis auritus*), readily take advantage of suitable hydrologic conditions for nest construction but also may have multiple spawning bouts if nests are destroyed (Lukas and Orth 1993). Traits representing the timing of spawning (e.g., winter spawners) were correlated to many hydrologic variables that reflected high or low seasonal magnitudes. For instance, summer spawners were positively correlated to the number of zero-flow days and low-flow frequencies, whereas spring spawners were negatively associated with higher spring flows but positively associated with higher winter flows. Bearers, open substrate spawners, and substrate choosers were poorly correlated with hydrologic variables; however, substrate choosers did show negative correlations with short-duration high flows, daily flow variation, and rise/fall rates.

Distinguishing the role of hydrology from other variables

Many complications arise in attempting to tease apart individual variable importance in structuring fish

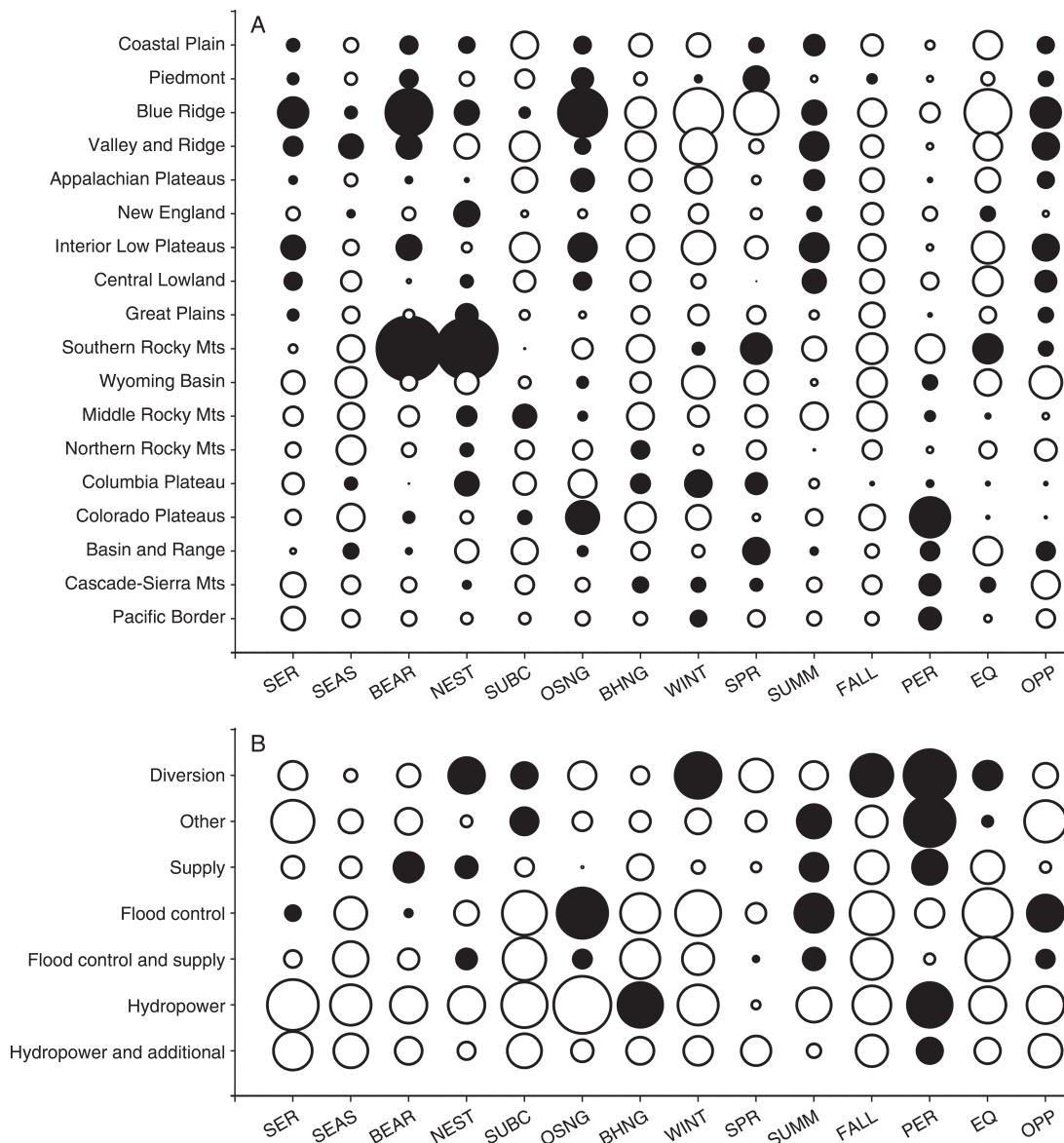


FIG. 7. Predicted positive (white) and negative (black) shifts in trait frequencies following dam regulation according to (A) physiographic provinces and (B) dam purposes. Responses represent average response values for each class divided by standard deviation and were predicted using the hydrologic-variable model for all fish. Mts stands for mountains. See Fig. 4 for definition of other abbreviations.

assemblages because of issues related to scale, hierarchy, and interactions among abiotic factors (Jackson et al. 2001). This is especially true for hydrology, because it operates at multiple spatial and temporal scales (Olden et al. 2012), and its interaction with other variables in shaping fish community composition also depends upon scale (Marsh-Mathews and Mathews 2000). This was evident by the strong correlations between hydrologic and landscape variables and the considerable amount of variation comprised by their combined effects. Depending on the analysis, the variance explained by hydrology alone was significant and comparable to that of

landscape variables. While this obviously suggests that hydrology plays a role in shaping the composition of fish communities, the perceived overlap among variables is the result of a mechanistic or hierarchical association. At the continental scale, landscape variables control variation in hydrology (Carlisle et al. 2010), which then exert selective pressures on fish assemblages. As an example, underlying bedrock lithology determines the physiochemical characteristics of water bodies while also influencing hydrology (Lindsey et al. 2009). Likewise, areas of similar climatic, topographic, and geomorphic types have been used to stratify hydrologic regime types

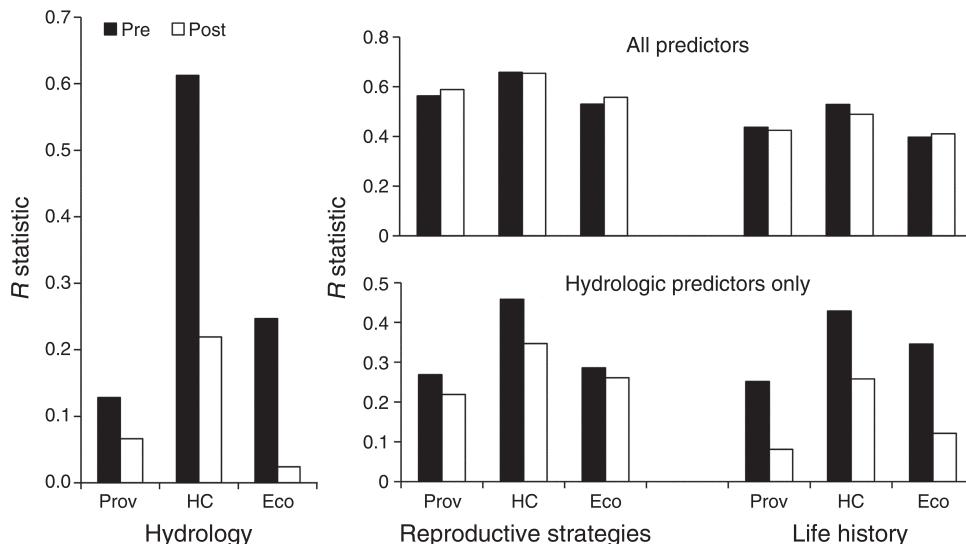


FIG. 8. Regional distinctness in hydrology, reproductive strategies, and life history groups for pre- and post-dam-regulation scenarios as measured by ANOSIM R statistics. Regional distinctness was measured using rank dissimilarities in hydrology and predicted trait-responses among physiographic provinces (Prov), hydrologic classes (HC), and ecoregions (EC).

(Morris et al. 2009, Knight et al. 2012) and hydrology–stream morphology relationships (Johnson and Fecko 2008). However, there are likely other nonhydrologic variables that serve as mediator variables between landscape controls and fish assemblages. For example, topography and geology exert controls on aquatic habitat structure, such as gradient, riffle-pool sequences, and substrate structure (Jackson et al. 2001), whereas ecosystem productivity (i.e., net carbon production), a function of climate and geology, has been shown to be positively related with fish diversity (Guégan et al. 1998) and negatively related to the proportion of equilibrium species (Olden and Kennard 2010).

The perceived importance of hydrology in structuring fish assemblages also depends on the spatial and temporal scale chosen by the investigator (Jackson et al. 2001). The hydroclimatic context may filter which regional species are found in the local species pool; however, individual streams may also have their own unique hydrologic signature within the surrounding hydroclimatic context (McManamay et al. 2012b). Marsh-Mathews and Mathews (2000) concluded that broad geographic variables, as opposed to localized habitat variables (such as flow variation), plays a large role in structuring fish assemblage composition in the midwestern United States. However, latitude is a robust predictor of major hydrologic types (McManamay et al. 2012b, 2014); thus, the documented importance of environmental factors, including hydrology, is largely an artifact of how they are classified and measured. While the persistence of species within a stream system or basin may be dependent upon hydrologic patterns over years or decades, respectively (Jackson et al. 2001, Herbert and Gelwick 2003, Olden and Kennard 2010), changes in hydrology over the course of hours may

influence fish behavior (Schwartz and Herricks 2005, Thompson et al. 2011), whereas hydrologic variation over days and months influence growth (Peterson and Jennings 2007). Thus, when suggesting the relative importance of hydrology compared to other variables, transparency is needed in how hydrology factors are calculated and summarized.

Implications of stream flow alteration on fish assemblages

After applying predictive models to dam regulated hydrology, we observed consistent, albeit small, predicted shifts in life history traits. In agreement with the existing literature (Winemiller 2005, Mims and Olden 2012, 2013), increases in the proportion of equilibrium strategists followed hydrologic changes induced by dam regulation. Consistent decreases in daily variation in flow and increases in low flows and baseflows suggests more stable environments, which are favorable to the equilibrium strategy (Winemiller and Rose 1992). In contrast, net decreases in periodic and opportunistic strategies, although variable, were also predicted based on our model. In accordance with our findings, Mims and Olden (2013) found higher proportions of equilibrium species and lower proportions of opportunistic species below dams compared to unregulated nearby locations. In contrast to our study, periodic species showed no difference between regulated or unregulated systems (Mims and Olden 2013).

Reproductive strategies also responded predictably to dam regulation; however, responses were more variable than life history groups and only significant in hydrologic variable models. Increases in the stability of harsh environments were predicted to decrease serial spawners, nest guards, and summer spawners. Conversely, increases in brood hidiers and substrate choosers were

predicted due to the same reasons. Predicted increases in winter and fall spawners were unexpected given little correlation between these traits and monthly flows. However, increases in these traits were likely due to decreases in high flows and decreased high-flow frequencies as opposed to changes in monthly flows. In general, dam regulation tends to stabilize seasonal variation by moderating extremities, either through decreasing peak flows (Fitzgugh and Vogel 2011) and/or increasing low flows (Poff et al. 2007). Given the seasonal stabilization, predicted increases in spawning season length make intuitive sense.

Trade-offs among the expression of various traits (i.e., tactics) produce suites of common life history strategies, some of which are favored under various environmental conditions (Southwood 1988). Adaptive strategies of fish assemblages, measured as trait-frequencies, are an artifact of selective pressures imposed by continental-wide gradients in hydrologic conditions (Schlosser 1987, 1990, Jackson and Harvey 1989, Tonn 1990). Thus, if natural hydrologic variation operates at multiple scales to filter the regional species pool and hence, shape fish assemblage composition (Jackson et al. 2001), then widespread modifications to natural hydrology also impose an environmental filter by exerting a different suite of selective pressures, in which endemic fish are maladapted. Dam regulation alters the existing hydrologic filter by removing the hydrologic uniqueness of regionally distinct stream flows (Poff et al. 2007) and selecting for life history strategies adapted to take advantage of more stable and predictable environments (Olden et al. 2006, Mims and Olden 2012). Similar to Poff et al. (2007), we observed consistent losses in the regional distinctness of hydrologic patterns, suggesting a homogenization of hydrology. Based solely on hydrologic changes, regional dissimilarities in reproductive strategies and life history groups were predicted to decrease following dam regulation. However, these predictions were observed with the all-variable model, which suggests that the relative role of nonhydrologic variables may be important in determining the full ecological effects of hydrologic disturbance.

Although some generalities in hydrologic and ecological responses to dam regulation can be inferred, predicted shifts in life histories and reproductive strategies were highly variable, even within similar geographical locations (Figs. 6, 7). Hydrology displays consistent responses to disturbance within regions (Poff et al. 2007) or hydrologic classes (McManamay et al. 2012a); thus, it follows that ecological responses to altered hydrology could also be organized by a similar framework (Poff et al. 2010). Our results suggest that hydrologic classes and provinces may provide a geographical context, whereas dam purpose may provide an operational context to evaluate trait responses to dam regulation. However, considerable unexplained variation in trait responses across classes suggests that ecological responses to dam regulation is complex and

will likely require intensive model building to quantify. Furthermore, simplified frameworks will be insufficient for evaluating ecological responses to multifaceted disturbances if used in isolation.

Limitations of our approach

Using large-scale hydrology-trait models to predict ecological responses to hydrologic alteration does not come without limitations. In order to understand how hydrology shapes the trait characteristics of local species pools, we summarized hydrologic variables and trait frequencies within HUC8 watersheds as opposed to using local stream network data. Similar to Smith and Powell (1971) and Jackson et al. (2001), we view the local species pool (i.e., within a basin) as an artifact of climatic filtering of the regional species pool, where regional species pools are a product of coarser geographic filtering. Local communities (as opposed to local species pool) are not only shaped by the surrounding geographic and hydroclimatic context, but also a multitude of other abiotic or biotic factors operating at the local scale (Jackson et al. 2001). In addition, using local analyses to infer continental patterns can be problematic because sampled sites may not be representative of the entire fish species pool. However, for the above reasons, we urge caution in relying on coarse models to predict the ecological effects of hydrologic alteration at a given location. Our models predict shifts in trait frequencies, or niche space, as opposed to predicting species presence or absence in local communities. Because predicting extinction and colonization require analyses at the local community level, an appropriate interpretation is to view shifts in trait frequencies as changes in selection pressures. While dams may vary in their individual hydrologic signatures, the hydrologic effects of dams may be consistent within a geographic region (Poff et al. 2007, McManamay et al. 2012a) and lead to continental-wide changes in trait frequencies. Thus, the models we present may be used to infer shifts in niche space within and among regions, but not specific locations.

Another dispute that may arise with our approach is using gage data from dendritic stream networks to summarize hydrologic variation within hydrologic units. However, using local stream gage data to infer larger scale patterns in hydroclimatic variation is a common approach in environmental flow management (Poff et al. 2010), including summarizing discharge information from stream gages into runoff estimates for HUC8 hydrologic units (*available online*)⁶ and creating hydrologic classifications, i.e., grouping streams by similarities in stream flow (Haines et al. 1988, Burn and Arnell 1993, Poff 1996). In addition, all magnitude-related variables were standardized to account for differences in river size; thus, summaries of hydrologic variation within hydro-

⁶ <http://waterwatch.usgs.gov/index.php?id=romap3>

logic units should not be influenced by differences in flow magnitudes.

One limitation of using existing patterns in endemic trait frequencies to predict the ecological consequences of hydrologic alteration is that this approach does not explicitly account for extinction and colonization dynamics by endemic and invasive species, respectively. Predicting trait-frequency responses strictly on the basis of hydrologic change can isolate the effect of hydrology independent of other factors that accompany dam regulation, such as temperature alteration (Olden and Naiman 2010), losses to habitat heterogeneity (Moyle and Mount 2007), and stocking (Mims and Olden 2012). However, the true composition of hydrologically altered fish communities is an artifact of all of the above, as well as extinction of fishes maladapted to the new conditions or outcompeted by new colonists (Olden et al. 2006) and successful invasions by nonnative species (Fausch et al. 2001, Olden et al. 2006).

Within our modeling approach, the same temporal scale used to develop natural hydrology-trait relationships was also applied to predict trait responses to dam regulation. However, there may be a disconnection between the temporal and spatial scales in which natural and altered hydrology operate to influence fish assemblages. While species pools are an artifact of long-term climatic filtering through natural selection (Tonn 1990), disturbances, such as urbanization and hydropower peaking, cause abrupt, unnatural hydrologic changes over short temporal scales and induce conditions in which natural fish communities are maladapted. For example, many studies have assessed the impacts of subdaily flow variation from hydropower peaking on fish assemblages (for a review, see Cushman [1985]; also see Lauters et al. [1996], Bradford [1997], Saltviet et al. [2001]); however, very few studies have evaluated relationships between fish and natural subdaily flow variation (David and Closs 2002, Schwartz and Herricks 2005, Thompson et al. 2011). Thus, predicting the full ecological consequences of these types of disturbance may not be feasible using only natural hydrology-trait relationships.

CONCLUSIONS

Ultimately, the relatively high predictive capacity of hydrologic models in explaining variation in fish trait frequencies suggests that hydrology does play a role in shaping fish communities at the continental scale through selective pressures. However, isolating the role of hydrology is complicated by multiple interrelationships with other geographic variables and those relationships change with scale. To avoid inconsistency in documented results, we suggest that the spatial and temporal scales used to isolate ecological responses to altered hydrology should be placed within the same spatiotemporal context of natural hydrology-trait relationships as to have a proper understanding of the role of hydrology relative to scale. Much of the current

scientific understanding of the importance of hydrology to river communities is based upon ecological responses to hydrologic alteration (i.e., disturbed ecosystems; Poff et al. 2010, Poff and Zimmerman 2010). However, predicting ecological responses to future disturbances, such as climate change, proves difficult when relying on empirical relationships. While examples of ecological consequences to drastic hydrologic alterations are more abundant (Poff et al. 2010), little empirical evidence is available for assessing ecological responses to small to moderate hydrologic changes (Harvey et al. 2014). Thus, understanding how natural hydrology structures biotic communities in river systems provides a framework to make future projections under a range of hydrologic alteration scenarios.

Despite the coarse spatial resolution of our models, we observed predicted shifts in fish life history strategies and reproductive strategies post-dam-regulation that were in accordance with the existing theories of fish adaptive strategies to environmental conditions. Our results also suggest that losses in regionally distinct hydrologic regimes may lead to a homogenization of fish life histories and reproductive strategies due to dam regulation. Utilizing trait frequencies provides a theoretical framework for creating and testing new hypotheses regarding the role of hydrology in shaping fish communities. Because ecological responses to hydrologic alterations are likely to be highly heterogeneous, we suggest that models with the explicit purpose of isolating hydrologic controls on ecological phenomena should account for geographic context and interacting abiotic and biotic confounding factors depending upon the scale of application. In addition, more local-level analyses that consider the multidimensional nature of hydrologic disturbances, such as water quality, are needed for making more accurate localized predictions. Furthermore, field studies are essential to validate hydrology-ecology model predictions.

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LITERATURE CITED

- Balon, E. K. 1975. Reproductive guilds in fishes: a proposal and definition. *Journal of the Fisheries Research Board of Canada* 32:821–864.
- Blank, A., P. A. Tedesco, and N. Lamouroux. 2007. Relationships between life-history strategies of European

- freshwater fish species and their habitat preferences. *Freshwater Biology* 52:843–859.
- Bradford, M. J. 1997. An experimental study of stranding of juvenile salmonids on gravel bars and in side channels during rapid flow decreases. *Regulated Rivers: Research and Management* 13:395–401.
- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.
- Burn, D. H., and N. W. Arnell. 1993. Synchronicity in global flood responses. *Journal of Hydrology* 144:381–404.
- Carlisle, D. M., J. Falcone, D. M. Wolock, M. R. Meador, and R. H. Norris. 2010. Predicting the natural flow regime: models for assessing hydrological alteration in streams. *Rivers Research and Applications* 26:118–136.
- Carlisle, D. M., D. M. Wolock, and M. R. Meador. 2011. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment* 9:264–270.
- Cole, L. 1954. The population consequences of life history phenomena. *Quarterly Review in Biology* 29:103–137.
- Craven, S. W., J. T. Peterson, M. C. Freeman, T. J. Kwak, and E. Irwin. 2010. Modeling the relations between flow regime components, species traits, and spawning success of fish in warmwater streams. *Environmental Management* 46:181–194.
- Cushman, R. M. 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *North American Journal of Fisheries Management* 5:330–339.
- Cutler, D. R., T. C. Edwards, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. *Ecology* 88:2783–2792.
- David, B. O., and G. P. Closs. 2002. Behavior of a stream-dwelling fish before, during, and after high-discharge events. *Transactions of the American Fisheries Society* 131:762–771.
- Diniz-Filho, J. A. F., C. E. R. de Sant'Ana, and L. M. Bini. 1998. An eigenvector method for estimating phylogenetic inertia. *Evolution* 52:1247–1262.
- Falcone, J. A., D. M. Carlisle, and L. C. Weber. 2010a. Quantifying human disturbance in watersheds: variable selection and performance of a GIS-based disturbance index for predicting the biological condition of perennial streams. *Ecological Indicators* 10:264–273.
- Falcone, J. A., D. M. Carlisle, D. M. Wolock, and M. R. Meador. 2010b. GAGES: a stream gage database for evaluating natural and altered flow conditions in the conterminous United States. *Ecology* 91:621.
- Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. *Ecological Applications* 11:1438–1455.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Midland Naturalist* 125:1–15.
- Fenneman, N. M., and D. W. Johnson. 1946. Physiographic divisions of the conterminous US. Scale 1:7,000,000. U.S. Geological Survey Special Map Series, Reston, Virginia, USA.
- Fitzhugh, T. W., and R. M. Vogel. 2011. The impact of dams on flood flows in the United States. *River Research and Applications* 27:1192–1215.
- Freeman, M. C., and G. D. Grossman. 1993. Effects of habitat availability on dispersion of a stream cyprinid. *Environmental Biology of Fishes* 37:121–130.
- Frimpong, E. A., and P. L. Angermeier. 2009. FishTraits: a database of ecological and life-history traits of freshwater fishes of the United States. *Fisheries* 34:487–495.
- Frimpong, E. A., and P. L. Angermeier. 2010a. Comparative utility of selected frameworks for regionalizing fish-based bioassessments across the United States. *Transactions of the American Fisheries Society* 139:1872–1895.
- Frimpong, E. A., and P. L. Angermeier. 2010b. Trait based approaches in the analysis of stream fish communities. Pages 109–136 in K. B. Gido and D. A. Jackson, editors. *Community ecology of stream fishes: concepts, approaches, and techniques*. American Fisheries Society, Symposium 73, Bethesda, Maryland, USA.
- Froese, R., and D. Pauly. 2013. FishBase. www.fishbase.org
- Goldstein, R. M., and M. R. Meador. 2004. Comparisons of fish species traits from small streams to large rivers. *Transactions of the American Fisheries Society* 133:971–983.
- Grabowski, T. B., and J. J. Isely. 2007. Effects of flow fluctuations on the spawning habitat of a riverine fish. *Southeastern Naturalist* 6:471–478.
- Growns, I. 2004. A numerical classification of reproductive guilds of freshwater fishes of south-eastern Australia and their application to river management. *Fisheries Management and Ecology* 11:369–377.
- Guégan, J. F., S. Lek, and T. Oberdorff. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature* 391:382–384.
- Haines, A. T., B. L. Findlayson, and T. A. McMahon. 1988. A global classification of river regimes. *Applied Geography* 8:255–272.
- Harvey, B. C., J. L. White, R. J. Nakamoto, and S. F. Railsback. 2014. Effects of streamflow diversion on a fish population: combining empirical data and individual-based models in a site-specific evaluation. *North American Journal of Fisheries Management* 34:247–257.
- Hastings, D. A., et al. 1999. The global land one-kilometer base elevation (GLOBE) digital elevation model, Version 1.0. National Oceanic and Atmospheric Administration, National Geophysical Data Center, Washington, D.C., USA. <http://www.ngdc.noaa.gov/mgg/topo/globe.html>
- Henriksen, J. A., J. Heasley, J. G. Kennen, and S. Nieswand. 2006. Users' manual for the hydroecological integrity assessment process software (including the New Jersey assessment tools). U.S. Geological Survey Report 2006-1093. U.S. Geological Survey, Reston, Virginia, USA.
- Herbert, M. E., and F. P. Gelwick. 2003. Spatial variation of headwater fish assemblages explained by hydrologic variability and upstream effects of impoundment. *Copeia* 2003:273–284.
- Imhoff, M. L., L. Bounoua, T. Ricketts, C. Loucks, R. Harriss, and W. T. Lawrence. 2004. Global patterns in net primary productivity. <http://sedac.ciesin.columbia.edu/es/hanpp.html>
- Jackson, D. A. 1993. Stopping rules in principal components-analysis—a comparison of heuristic and statistical approaches. *Ecology* 74:2204–2214.
- Jackson, D. A., and H. H. Harvey. 1989. Biogeographic associations in fish assemblages: local vs. regional processes. *Ecology* 70:1472–1484.
- Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities—the roles of biotic, abiotic and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:157–170.
- Johnson, P. A., and B. J. Fecko. 2008. Regional channel geometry equations: a statistical comparison for physiographic provinces in the Eastern US. *River Research and Applications* 24:823–834.
- Kennard, M. J., S. J. Mackay, B. J. Pusey, J. D. Olden, and N. Marsh. 2010. Quantifying uncertainty in estimation of hydrologic metrics for ecohydrological studies. *River Research and Applications* 26:137–156.
- King, J. M., J. A. Cambray, and D. N. Impson. 1998. Linked effects of dam-released floods and water temperature on spawning of the Clanwilliam yellowfish *Barbus capensis*. *Hydrobiologia* 384:245–265.
- Knight, R. R., W. S. Gain, and W. J. Wolfe. 2012. Modeling ecological flow regime: an example from the Tennessee and Cumberland River basins. *Ecohydrology* 5:613–627.

- Knight, R. R., M. B. Gregory, and A. K. Wales. 2008. Relating streamflow characteristics to specialized insectivores in the Tennessee River Valley: a regional approach. *Ecohydrology* 1:394–407.
- Lauters, F., P. Lavandier, P. Lim, C. Sabaton, and A. Belaud. 1996. Influence of hydropeaking on invertebrates and their relationship with fish feeding habitats in a Pyrenean River. *Regulated Rivers: Research and Management* 12:563–573.
- Leitman, H. M., M. R. Darst, and J. J. Nordhaus. 1991. Fishes in the forested floodplain of the Ochlockonee River, Florida, during flood and drought conditions. Report 90-4204. U.S. Geological Survey Water-Resources Investigations, Tallahassee, Florida, USA.
- Light, H. M., M. R. Darst, and J. W. Grubbs. 1998. Aquatic habitats in relation to river flow in the Apalachicola River floodplain, Florida. U.S. Geological Survey Professional Paper 1594. U.S. Geological Survey, Reston, Virginia, USA.
- Lindsey, B. D., M. P. Berndt, B. G. Katz, A. F. Ardis, and K. A. Skach. 2009. Factors affecting water quality in selected carbonate aquifers in the United States, 1993–2005. U.S. Geological Survey Scientific Investigations Report 2008-5240. U.S. Geological Survey, Reston, Virginia, USA.
- Lukas, J. A., and D. J. Orth. 1993. Reproductive ecology of redbreast sunfish *Lepomis auritus* in a Virginia stream. *Journal of Freshwater Ecology* 8:235–244.
- Marsh-Mathews, E., and W. J. Mathews. 2000. Geographic, terrestrial and aquatic factors: which most influence the structure of stream fish assemblages in the midwestern United States? *Ecology of Freshwater Fish* 9:9–21.
- McCune, B., and J. Grace. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon, USA.
- McManamay, R. A., M. S. Bevelhimer, and S. Kao. 2014. Updating the US hydrologic classification: an approach to clustering and stratifying ecohydrologic data. *Ecohydrology* 7:903–926.
- McManamay, R. A., D. J. Orth, and C. A. Dolloff. 2012a. Revisiting the homogenization of dammed rivers in the southeastern US. *Journal of Hydrology* 424–425:217–237.
- McManamay, R. A., D. J. Orth, C. A. Dolloff, and E. A. Frimpong. 2012b. A regional classification of unregulated streamflows: spatial resolution and hierarchical frameworks. *River Research and Applications* 28:1019–1033.
- McManamay, R. A., D. J. Orth, J. Kauffman, and M. D. Davis. 2013. A database and meta-analysis of ecological responses to flow in the South Atlantic Region. *Southeastern Naturalist* 12(Monograph 5):1–36.
- Mims, M. C., and J. D. Olden. 2012. Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology* 93:35–45.
- Mims, M. C., and J. D. Olden. 2013. Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshwater Biology* 58:50–62.
- Mims, M. C., J. D. Olden, Z. R. Shattuck, and N. L. Poff. 2010. Life history trait diversity of native freshwater fishes in North America. *Ecology of Freshwater Fish* 19:390–400.
- Morris, A. J., J. J. Donovan, and M. Strager. 2009. Geospatial analysis of climatic and geomorphic interactions influencing stream discharge, Appalachian Mountains, USA. *Environmental Modelling and Assessment* 14:73–84.
- Moyle, P. B., and J. F. Mount. 2007. Homogenous rivers, homogenous faunas. *Proceedings of the National Academy of Sciences USA* 104:5711–5712.
- MRLC (Multi-Resolution Land Characteristics Consortium). 2013. National land cover database. <http://www.mrlc.gov/>
- NatureServe. 2004. Downloadable animal datasets. NatureServe Central Databases. www.natureserve.org/getData/dataSets/watershedHucs/index.jsp
- Nelson, J. S. 2006. *Fishes of the world*. Fourth edition. Wiley, New York, New York, USA.
- Nesler, T. P., R. T. Muth, and A. F. Wasowicz. 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. *Transactions of the American Fisheries Society Symposium* 5:6:8–79.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. *vegan: community ecology package*. <http://cran.r-project.org/web/packages/vegan/index.html>
- Olden, J. D., and M. J. Kennard MJ. 2010. Intercontinental comparison of fish life history strategies along a gradient of hydrologic variability. Pages 109–136 in K. B. Gido and D. A. Jackson, editors. *Community ecology of stream fishes: concepts, approaches, and techniques*. American Fisheries Society Symposium 73, Bethesda, Maryland, USA.
- Olden, J. D., M. J. Kennard, and B. J. Pusey. 2012. A framework for hydrologic classification with a review of methodologies and applications in ecohydrology. *Ecohydrology* 5:503–518.
- Olden, J. D., and R. J. Naiman. 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology* 55:86–107.
- Olden, J. D., and N. L. Poff. 2003. Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications* 19:101–121.
- Olden, J. D., N. L. Poff, and K. R. Bestgen. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs* 76:25–40.
- Page, L. M., and B. M. Burr. 1991. *A field guide to freshwater fishes of North America north of Mexico*. Houghton Mifflin Company, Boston, Massachusetts, USA.
- Peterson, R. C., and C. A. Jennings. 2007. Effects of river discharge on abundance and instantaneous growth of age-0 carpsuckers in the Oconee River, Georgia, USA. *River Research and Applications* 23:1016–1025.
- Poff, N. L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology* 36:71–91.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and in stream ecology. *Journal of the North American Benthological Society* 16:391–409.
- Poff, N. L., and J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76:606–627.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience* 47:769–784.
- Poff, N. L., and D. D. Hart. 2002. Dams vary and why it matters. *BioScience* 52:659–668.
- Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences USA* 104:5732–5737.
- Poff, N. L., et al. 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biology* 55:147–170.
- Poff, N. L., and J. Z. H. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* 55:194–205.
- PRISM (PRISM Climate Group). 2013. PRISM climate data. Northwest Alliance for Computational Science and Engineering (NACSE). Oregon State University, Corvallis, Oregon, USA. <http://www.prism.oregonstate.edu/>
- Pyron, M., and T. E. Lauer. 2004. Hydrologic variation and fish assemblage structure in the middle Wabash River. *Hydrobiologia* 525:203–213.

- Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* 10:1163–1174.
- Richter, B. D., J. V. Baumgartner, R. Wigington, and D. P. Braun. 1997. How much water does a river need? *Freshwater Biology* 37:231–249.
- Schlosser, I. J. 1987. The role of predation in age- and size-related habitat use by stream fishes. *Ecology* 68:651–659.
- Schlosser, I. J. 1990. Ecological variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. *Environmental Management* 14:621–628.
- Schwartz, J. S., and E. E. Herricks. 2005. Fish use of stage-specific fluvial habitats as refuge patches during a flood in a low-gradient Illinois stream. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1540–1552.
- Smith, C. L., and C. R. Powell. 1971. The summer fish communities of Brier Creek, Marshall County, Oklahoma. *American Museum Novitates* 2458:1–30.
- Southwood, T. R. E. 1988. Tactics, strategies and templets. *Oikos* 52:3–18.
- Stevens, M. H. H., and J. Oksanen. 2012. Permutational multivariate analysis of variance using distance matrices. Package *vegan*. <http://cc.oulu.fi/~jarioksa/softhelp/vegan/html/adonis.html>
- Tedesco, P., B. Huguency, T. Oberdorff, H. H. Durr, S. Merigoux, and B. de Merona. 2008. River hydrological seasonality influences life history strategies of tropical riverine fishes. *Oecologia* 156:691–702.
- Thompson, L. C., S. A. Cocherell, S. N. Chun, J. J. Cech, and A. P. Klimley. 2011. Longitudinal movement of fish in response to a single-day flow pulse. *Environmental Biology of Fish* 90:253–261.
- Tonn, W. M. 1990. Climate change and fish communities: a conceptual framework. *Transactions of the American Fisheries Society* 119:337–352.
- Trush, W. J., S. M. McBain, and L. B. Leopold. 2000. Attributes of an alluvial river and their relation to water policy and management. *Proceedings of the National Academy of Sciences USA* 97:11858–11863.
- Vogl, A. L., and V. L. Lopes. 2009. Impacts of water resources development on flow regimes in the Brazos River. *Environmental Monitoring and Assessment* 157:331–345.
- Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* 62:872–885.
- Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implication for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2196–2218.
- Wolock, D. M., T. C. Winter, and G. McMahon. 2004. Delineation and evaluation of hydrologic landscape regions in the United States using geographic information system tools and multivariate statistical analyses. *Environmental Management* 34:S71–S88.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D are available online: <http://dx.doi.org/10.1890/14-0247.1.sm>

Data Availability

Data associated with this paper have been deposited in Oak Ridge National Laboratory's National Hydropower Asset Assessment Program: <http://nhaap.ornl.gov/NHAAP-GIS-Data-and-Maps>