

Associations among hydrologic classifications and fish traits to support environmental flow standards

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ABSTRACT

Classification systems are valuable to ecological management in that they organize information into consolidated units thereby providing efficient means to achieve conservation objectives. Of the many ways classifications benefit management, hypothesis generation has been discussed as the most important. However, in order to provide templates for developing and testing ecologically relevant hypotheses, classifications created using environmental variables must be linked to ecological patterns. Herein, we develop associations between a recent US hydrologic classification and fish traits in order to form a template for generating flow–ecology hypotheses and supporting environmental flow standard development. Tradeoffs in adaptive strategies for fish were observed across a spectrum of stable, perennial flow to unstable intermittent flow. In accordance with theory, periodic strategists were associated with stable, predictable flow, whereas opportunistic strategists were more affiliated with intermittent, variable flows. We developed linkages between the uniqueness of hydrologic character and ecological distinction among classes, which may translate into predictions between losses in hydrologic uniqueness and ecological community response. Comparisons of classification strength between hydrologic classifications and other frameworks suggested that spatially contiguous classifications with higher regionalization will tend to explain more variation in ecological patterns. Despite explaining less ecological variation than other frameworks, we contend that hydrologic classifications are still useful because they provide a conceptual linkage between hydrologic variation and ecological communities to support flow–ecology relationships. Mechanistic associations among fish traits and hydrologic classes support the presumption that environmental flow standards should be developed uniquely for stream classes and ecological communities, therein. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS environmental flow; streams; water policy; aquatic conservation

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INTRODUCTION

The utility of classification systems in ecological management lies in their ability to consolidate substantial information into digestible units thereby providing a more efficient means to achieve conservation objectives. Specifically, classification systems are valuable in that they can be used to group sites with similar character (Frimpong and Angermeier, 2010a), stratify analyses for monitoring and/or experimentation (Wolock *et al.*, 2004), prioritize aquatic conservation areas (Snelder *et al.*, 2007), and generalize ecological responses to disturbances (Bailey, 1983). Melles *et al.* (2012) identify four key principles important to any classification system: Classifications should provide (1) a context for organizing information and making inductive generalizations about groups of observations, (2) a

consistent framework for communication, (3) a simplified method for understanding complex associations, and (4) a template for generating hypotheses. Sokal (1974) suggests that although classifications have many practical and applied outcomes, hypothesis generation is the greatest determinant of success.

Classifying streams or regions according to similarities in hydrology (i.e. hydrologic classifications) have been developed at a multitude of spatial scales from states to the globe depending on the context to suit research or management needs (e.g. Haines *et al.*, 1988; Poff, 1996; Wolock *et al.*, 2004; Sanborn and Bledsoe, 2006; Reidy Liermann *et al.*, 2012). Nationwide hydrologic classifications for the USA have varied from approaches deducing hydrologic regionality from landscape predictors (e.g. Wolock *et al.*, 2004) to inductive approaches using available hydrologic information to infer patterns in stream flow (e.g. Poff, 1996). With increases in the availability of hydrologic information (e.g. stream gauge data), inductive hydrologic classifications of streams have increased

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substantially in recent years (Olden *et al.*, 2012), with the most recent US continental classification created by (McManamay *et al.*, 2014). An immense amount of information is available to inform inductive hydrologic classification development, including the *a priori* selection of hydrologic metrics (Olden and Poff, 2003), the screening process for gauge selection (Falcone *et al.*, 2010; Kennard *et al.*, 2010a), developing linkages between classes and landscape patterns (Kennard *et al.*, 2010b; McManamay *et al.*, 2012), and a general overview of classification methods (Olden *et al.*, 2012). Despite the growing body of information on the process of creating hydrologic classifications, a far greater need is displaying the utility of hydrologic classifications once created. For example, we have observed little attention in the peer-reviewed literature in associating ecological characteristics with hydrological classes (except see Monk *et al.*, 2006; Chinnayakanahalli *et al.*, 2011; Rolls and Arthington, 2014).

The latest paradigm in environmental flow science is the development of the Ecological Limits of Hydrologic Alteration (ELOHA) framework (Poff *et al.*, 2010). The central design of ELOHA is based upon placing streams into hydrologic classes to provide a context for generalizing hydrologic disturbances, assembling and testing hypotheses regarding ecological responses to hydrologic disturbance, and lastly, developing environmental flow standards. In essence, hydrologic classifications form the template for developing hypothetical relationships between flow alteration and ecological responses (Arthington *et al.*, 2006). Comparisons of ecological patterns between natural and hydrologically altered streams within each class yield flow–ecological response relationships, which provide the basis for environmental flow standards (Arthington *et al.*, 2006). However, as a second step to creating stream classifications, Arthington *et al.* (2006) proposed that natural stream classes should be calibrated with empirically derived ecological data. We agree, because the ultimate goal of creating hydrologic classifications is to support the management of environmental flows and conservation efforts in rivers of different hydrological and ecological character. Understanding associations between ecological attributes of classes and distinguishing their hydrological characteristics can provide multiple beneficial outcomes including the following: (1) ensuring that classifications are ecologically relevant, i.e. whether variation in ecological patterns is explained by hydrologic classification systems, (2) refining classification solutions (e.g. number of classes) with ecological data, (3) drawing generalizations and inferences among class–ecology associations, and (4) most importantly, generating hypotheses regarding ecological responses to flow regime alterations within each hydrologic class. For hydrologic classifications to be incorporated as the underlying structure in developing environmental flow

standards, providing evidence of mechanistic associations between hydrologic classes and ecological patterns is necessary.

The primary purpose of this study was to develop associations between a recent hydrologic classification (McManamay *et al.*, 2014) and ecological characteristics in order to form a template for generating flow–ecology hypotheses and supporting environmental flow standard development. Across regions, the natural flow regime differs markedly in the magnitude, frequency, duration, timing, and rate of change of flow events, which shape the ecological communities adapted to survive in stream systems (Poff *et al.*, 1997; Bunn and Arthington, 2002). Conceivably, there is a wide array of ecological groups of interest that could potentially be linked to hydrologic classes. However, we focus on developing linkages between hydrologic variation and fish assemblages for three main reasons. First, many studies have shown that flow variability organizes fish assemblage structure (e.g. Poff and Allan, 1995; Jackson *et al.*, 2001; Herbert and Gelwick, 2003; Pyron and Lauer, 2004). Second, spatially contiguous distributions for all freshwater fish species were readily available for the conterminous USA (NatureServe, 2004), thereby providing an effective means to apply a multi-regional hydrologic classification to the entire fish assemblages. Lastly, trait information (ecological, life history, behavioural, and physiological adaptations to the environment) for the majority of freshwater fish species in North America was also available (Frimpong and Angermeier, 2009).

Traits are advantageous in large-scale analyses relating biotic responses to environmental variation because they consolidate information across many taxonomic groups into common adaptive strategies (Frimpong and Angermeier, 2009, 2010b). Fish traits have commonly been used in determining the role of habitat, landscape filters, and anthropogenic disturbances in shaping fish communities (Balon, 1975; Schlosser, 1990; Winemiller and Rose, 1992; Goldstein and Meador, 2004; Gowns, 2004; Blank *et al.*, 2007). With specific regard to hydrology, fish traits have been used to determine general relationships among flow and life history groups, reproductive strategies, habitat preferences, trophic status, and morphology (Poff and Allan, 1995; Pyron and Lauer, 2004; Craven *et al.*, 2010; Olden and Kennard, 2010; Carlisle *et al.*, 2011; Rolls and Arthington, 2014). Because of the broad conceptual basis behind the use of fish traits with relation to hydrology, we chose to apply our hydrologic classification to predicting patterns in fish life history groups and reproductive strategies across the landscape.

Recently, an inductive hydrologic classification for the entire USA was developed using stream gauge datasets of varying reference standards (McManamay *et al.*, 2014) (Figure 1, Table I). While multiple classification solutions

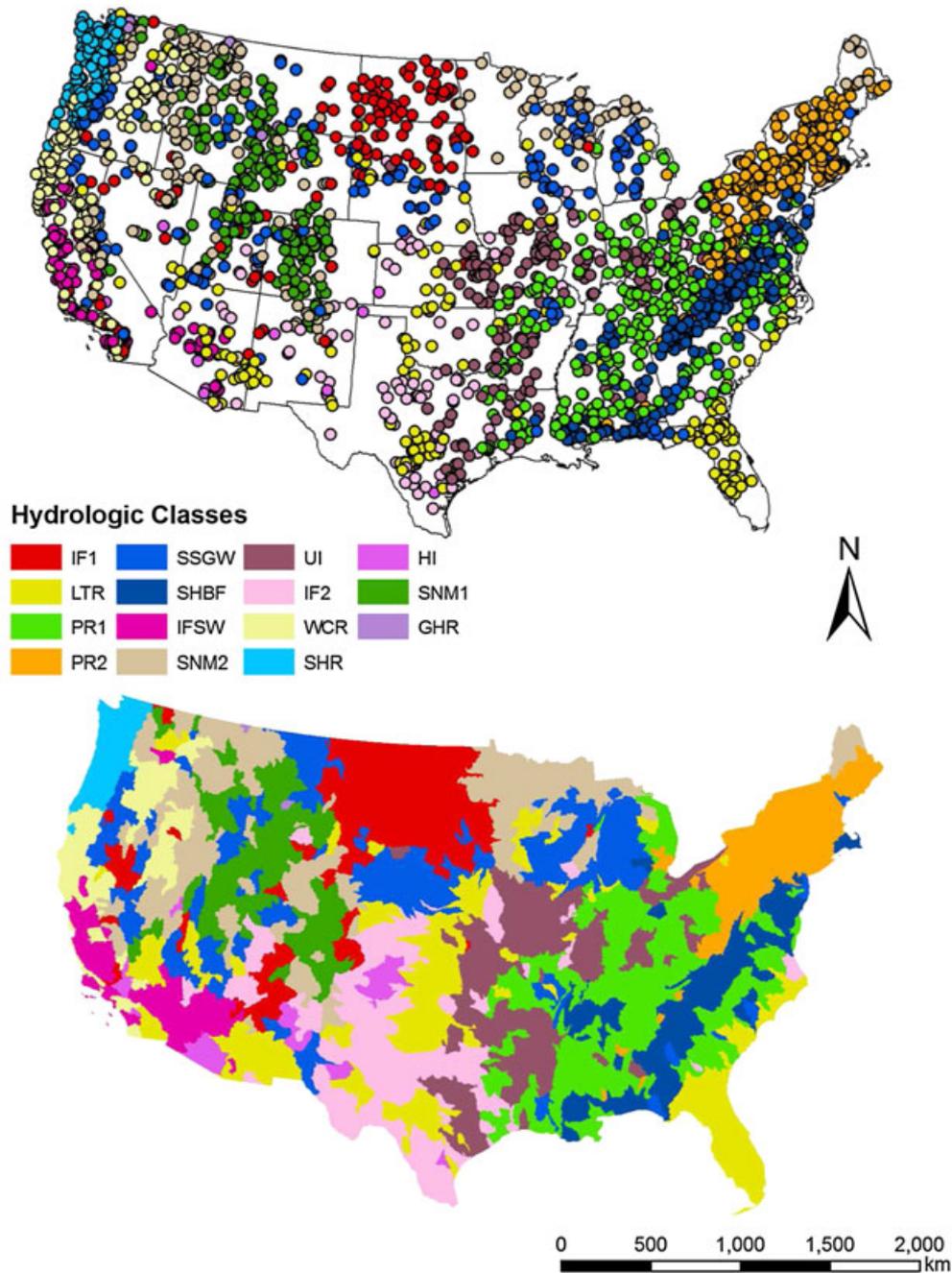


Figure 1. Hydrologic classification of 15 streamflow types for the USA (from McManamay *et al.*, 2014). Locations of stream gauges (top) are used to summarize hydrologic classes into hydrologic catalogue units (bottom). Class names are provided in Table I.

were available, we chose to evaluate the expanded hydrologic classification, represented by 15 classes, because it displayed higher regional affiliation and provided a more robust sample of natural flow variation across the USA despite being created with less-strict reference gauge criteria (Figure 1, Table I). We used a three-tiered approach to examine linkages between each hydrologic classification and fish traits. First, we examine how classes partition the multivariate trait space occupied

by fish assemblages across the USA and then examine the strength of trait associations with hydrologic gradients among classes. Second, in support of developing standards that protect the natural flow regime of river systems, we provide an approach to evaluate how hydrologic uniqueness translates to ecological uniqueness, which can be used to substantiate the use of hydrologic classes for environmental flow management. Finally, we compare the amount of variation in fish traits explained by the current US

Table I. Names and abbreviated codes used for hydrologic classes.

Hydrologic classes	Code
Intermittent flashy 1	IF1
Late timing runoff	LTR
Perennial runoff 1	PR1
Perennial runoff 2	PR2
Super stable groundwater	SSGW
Stable high baseflow	SHBF
Intermittent flashy SW	IFSW
Snowmelt 2	SNM2
Unpredictable intermittent	UI
Intermittent flashy 2	IF2
Western coastal runoff	WCR
Stable high runoff	SHR
Harsh intermittent	HI
Snowmelt 1	SNM1
Glacial high runoff	GHR

For detailed descriptions of classes see McManamay *et al.* (2014).

hydrologic classification to that of commonly used landscape classifications and determine whether alternative classification solutions could have improved ecological relevance.

METHODS

Assembling fish trait information

The US maps of spatial fish distributions of 865 freshwater species according to eight-digit hydrologic catalogue units (HUC-8) were available through NatureServe (NatureServe, 2004). We compiled the lists of all native fish species within each HUC-8. Fish traits were accessed through the FishTraits database, which contains trait-related information for 810 species of freshwater fish (Frimpong and Angermeier, 2009). Trait information for all species was not complete because of insufficient biological information. In addition, some fish species were not represented in FishTraits either because of occurring in estuaries, being highly endemic and not formally described, or differences in nomenclature and spelling. Estuarine fish were excluded from our analysis. For fish species without representative or complete trait information, we used NatureServe Explorer database, FishBase, literature searches, and general internet searches to update missing traits with new information or find the closest phylogenetic relative as a substitute for missing species or missing trait information. The closest phylogenetic relative was defined as (1) the closest clade or parental clade (subgenus), (2) a species in which potential hybridization could occur, or (3) species commonly misidentified as the species of interest (in that order of preference). Age-at-maturation, longevity, and fecundity

were highly related to maximum length (MAXTL) within the genus level. Because MAXTL was typically available, we used linear regression to predict missing information for some species.

We focused on fish traits that either could be used to summarize life history strategies or spawning characteristics, both of which have been linked to hydrologic variation (Olden and Kennard, 2010; Carlisle *et al.*, 2011). Life history traits included maximum length, age-at-maturation, longevity, and fecundity. Spawning characteristics included spawning strategies, spawning season timing and length, and whether fish had more than one spawning bout. Spawning strategies, represented as binary variables, ranged from no parental care (open-substratum broadcast spawning) to placing eggs in specific substrates (brood-hiders), to constructing nests and guarding young (substrate choosers and nest guards), and to bearing live young (bearers). Somewhat similar to Winemiller and Rose (1992), we calculated a parental care index 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 provided as a proportion for each month (January to December) within each species spawning season, whereas spawning season was provided as the sum of all monthly proportions (approximates the length of the spawning season). We calculated spawning seasonality indices by summing the proportions falling into different seasonal windows: Winter (December to February), Spring (March to May), Summer (June to August), and Fall (September to November). Serial spawners, species having more than one spawning bout, were denoted as binary variables. 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 environmental relationships with traits. FishTraits also includes a family number (from Nelson, 2006), which serves as a phylogenetic position of each family relative to other families (Frimpong and Angermeier, 2009). Smaller family numbers represent more primitive fishes. We accounted for the effect of family number on all traits by using generalized linear models (GLMs) with Gaussian, poisson, and binomial distributions, depending on the variable. After controlling for phylogenetic position using GLMs, we calculated deviance residuals for all variables to use in future analyses.

Winemiller and Rose (1992) identified three dominant life history groups for freshwater fish species, representing major endpoints in the continuum of tradeoffs among survival, growth, fecundity, and parental care. Periodic species are larger-bodied fish characterized by late maturation, high fecundity, and low parental investment. Equilibrium species are smaller-bodied, low fecundity fishes, which provide more parental care. Opportunistic

fishes, similar to r-strategists, are typically small-bodied fish with early maturation, no parental investment, and extended spawning seasons with multiple bouts. Similar to Mims *et al.* (2010), we 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. The periodic strategy endpoint consisted of 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 total length and longevity, maximum values for parental care and age-at-maturation, and minimum values for all other traits.

We summarized trait information for all historical and current fish species lists within each HUC-8 into composite values representing proportions or average deviance. For each HUC-8, we summarized the proportion of species as periodic, equilibrium, or opportunistic (Figure 2). All other traits were summarized as the average deviance value for all species present within a given HUC-8 (Figure 2).

Multivariate trends in fish traits

We explored the distribution of hydrologic classes within the multivariate space represented by fish traits and the importance of individual hydrologic indices in explaining variation in the multivariate space. We selected 37 hydrologic indices including the 33 Indicators of Hydrologic Alteration (Richter *et al.*, 1996), daily CV (Poff, 1996), mean annual runoff, high-flow frequency 2, and predictability (Table II). All magnitude-related indices were divided by the mean daily flow to account for differences in basin size. Hydrologic classes and hydrologic indices were assigned to HUC-8 watersheds within the conterminous USA using Arc GIS 9.3. We plotted each stream gauge by its latitude and longitude and constructed Thiessen polygons, which represent areas surrounding each gauge with boundaries equidistant from all neighbouring gauges. Using the identity function, the area represented by each gauge was calculated and used to represent the proportion of each HUC-8 represented by different hydrologic classes. The predominant hydrologic class and the mean values for hydrologic indices within each HUC-8 were also calculated. Many approaches could be used to assign hydrologic information to watersheds (e.g. predictive models); however, we favoured Thiessen polygons because they allowed flexibility in predicting hydrologic class in areas of limiting hydrologic information (low gauge density) and yet still sensitive to areas of overlapping hydrologic classes. Secondly, assembling variables within HUC-8 watersheds to predict hydrologic

class membership or indices would be inconsistent with the scale of models created using information summarized within the watershed of each gauge (e.g. some gauges span multiple HUC-8 watersheds).

Associations between fish traits and hydrologic classes were visually examined using a variety of methods. Box and whisker plots were used to evaluate patterns in traits among hydrologic classes, which were sorted along a gradient from high to low mean annual runoff. Ternary plots were used to examine the relative position of hydrologic classes within the trivariate life history space occupied by fish assemblages. Patterns of similarity in reproductive strategies among fish assemblages were visualized using principal components analysis (PCA) conducted on correlations among reproductive traits. All variables were $\log(x+1)$ transformed, centred to zero, and scaled prior to analysis. We used the broken-stick rule to determine the appropriate number of PCs to retain (Jackson, 1993). We plotted scores for first three PCs for all HUC-8 units in 3D space according to hydrologic class membership.

Mean values for all 14 traits and all 37 hydrologic indices were calculated for each hydrologic class. Spearman's rank correlations were then used to determine relationships between hydrologic indices and trait values using class averages as observations ($n=15$). The hydrologic indices with the highest correlations with each trait (ρ values >0.60) were selected.

Hydrologic and ecological distinction

Understanding the distinction among hydrologic classes should be relevant to management and future applications, such as linking classes to ecology. Furthermore, we questioned whether hydrologic distinction (multivariate class distance) was related to ecological distinction among classes. In order to determine relative levels of separation among the centroids of hydrologic classes, we calculated a hydrologic distinction matrix as squared Mahalanobis distances (D^2) between all pairwise class combinations. D^2 values represented the multivariate distances among class centroids and were calculated using the hydrologic variables mentioned previously. Hydrologic indices represented values directly from gauge data rather than data summarized by HUC. All magnitude-related indices were divided by the mean daily flow prior to analysis. We used the pooled covariance matrix, which ensures that distances among clusters are relative to the entire multivariate space comprised by all hydrologic classes.

We also calculated a fish-trait distinction matrix to assess the relative level of separation among fish traits according to hydrologic class membership. Using information from all HUC-8 watersheds, D^2 was calculated between all pairwise hydrologic class combinations using 14 fish traits. To ensure that variation in fish traits was due to hydrologic

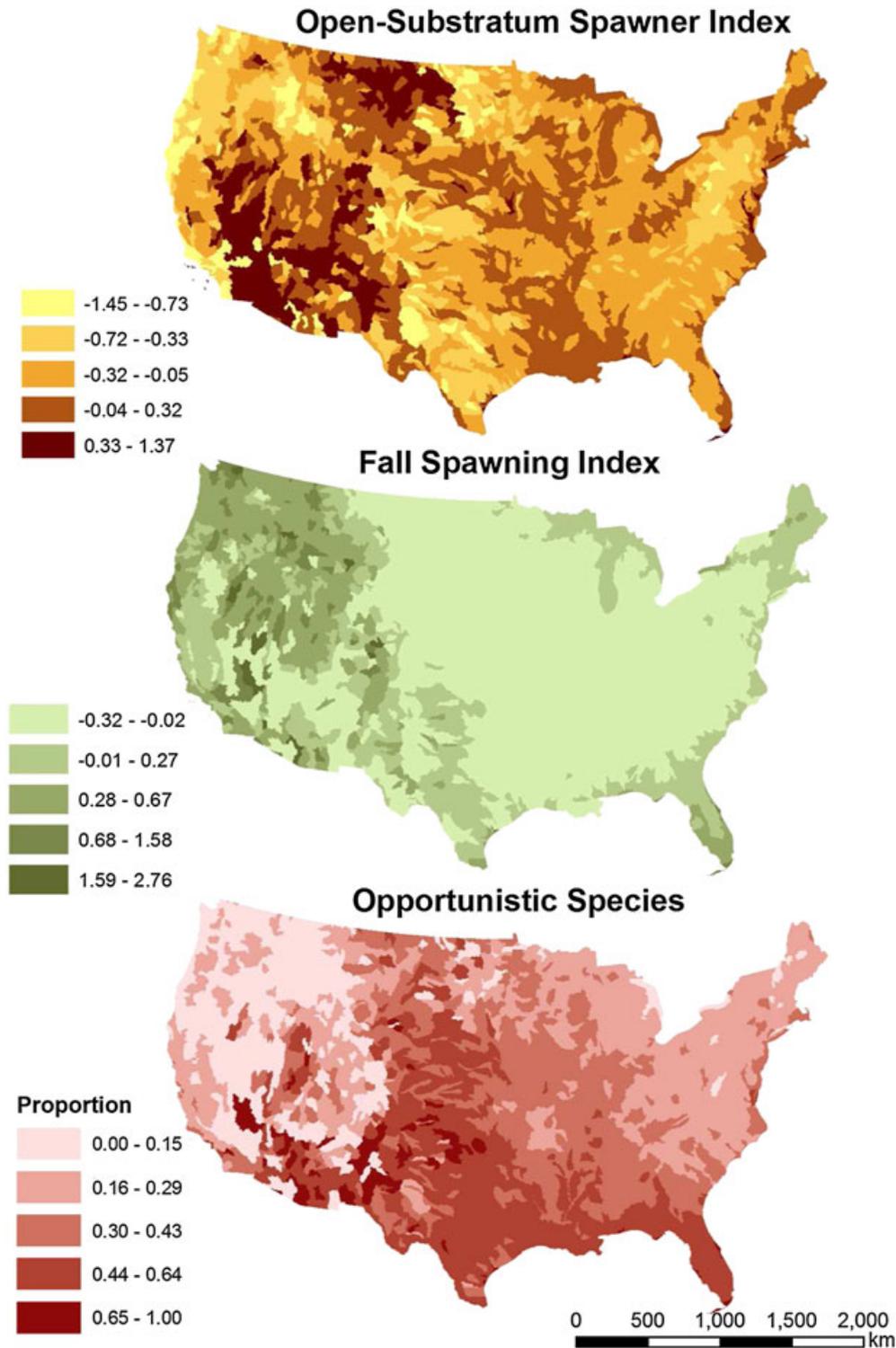


Figure 2. Examples of three fish traits summarized for all native species within 8-digit Hydrologic catalogue units in the conterminous USA. Trait indices (e.g. fall spawning index) were calculated as deviance residuals from linear models after controlling for phylogeny.

differences and not geographical separation, we calculated a geographic distance matrix as a control. Pairwise geographic distances were calculated as Euclidean distances using the centroids of the geographic distribution

hydrologic classes within HUC-8 watersheds. We used a Mantel test to compare the strength of the correlation between the fish trait distinction matrix and the hydrologic distinction matrix relative to the geographic distance

Table II. Thirty-seven hydrologic indices used in the analysis.

Variables	Description
Magnitude	
MA3	Daily coefficient of variation in flow
MA12–MA23	Mean monthly flows (January to December)
MA41	Mean annual runoff
ML17	Baseflow index
Duration	
DL1–DL5 ¹	Various duration low flows (1, 3, 7, 30, 90 days)
DL16	Low flow duration (duration of FL1)
DL18	Zero-flow days
DH1–DH5 ¹	Various duration high flows (1, 3, 7, 30, 90 days)
DH15	High flow duration (duration of FH1)
Frequency	
FL1	Low-flow frequency (<25% tile threshold)
FH1	High-flow frequency ¹ (>75% tile threshold)
FH6	High-flow frequency ² (>3× median flow)
Timing	
TA2	Predictability in flows
TL1	Julian date of annual minimum
TH1	Julian date of annual maximum
Rate of change	
RA1	Rise rate
RA3	Fall rate
RA8	Reversals

From Olden and Poff (2003).

matrix. The Mantel test was conducted in the R programming environment using the *ecodist* package and 1000 permutations (Goslee and Urban, 2014).

Classification strength

With regard to classification systems, classification strength refers to the proportion of total variance (R^2) in environmental characteristics explained by the classification system (e.g. Wolock *et al.*, 2004). As explained by Wolock *et al.* (2004), the effectiveness of classification systems can be measured by R^2 as an indication of the ability of the classes to separate environmental values into distinct groups. We compared the proportion of variation in fish traits explained by the hydrologic classification to three other widely used classification systems: Level II and III Ecoregions (Omernik, 1987), Hydrologic Landscape Regions (Wolock *et al.*, 2004), and physiographic provinces (Fenneman, 1946). All four classifications have been evaluated for their performance in predicting patterns in fish traits (Frimpong and Angermeier, 2010a). Ecoregions (EcoII and EcoIII) were delineated as areas with distinct abiotic (physiography and landuse) and biotic (ecological communities) on the basis of expert judgement (Omernik, 1987). Hydrologic Landscape Regions (HLRs) were created using variables that influence hydrology with the intent to stratify water-quality sites within different

hydrologic contexts (Wolock *et al.*, 2004). Physiographic provinces (Provinces) were created for mapping purposes as regions that share common topography and geomorphological structure and history (Fenneman, 1946). Because the predictive capacities of HLRs and Provinces have been utilized within hydrologic contexts (Mohamoud, 2008; Santhi *et al.*, 2008; Morris *et al.*, 2009), we questioned whether they would provide a comparable framework to flow classes in predicting fish traits.

The amount of variation explained by any landscape classification system will be reflected by the number of classes or regions, or degrees of freedom. Because ecoregions, HLRs, and provinces contain higher numbers of regions than hydrologic classes ($n=15$), a direct comparison would be biased. Varying the number of classes represented hydrologic variation would provide not only a method to produce comparable degrees of freedom but also a potential route to refine classification solutions. To vary the number of hydrologic classes, we produced 20 hydrologic classification solutions ranging from 5 to 100 classes, in multiples of 5. Using methods reported by McManamay *et al.* (2014), we reclassified streams by similarities in hydrology using a Gaussian mixture modelling approach. The approach assumes ten models with varying cluster structure and orientation (covariance structure) and then uses Bayesian criteria to identify the most likely model and number of clusters on the basis of maximum likelihood of parameter estimates (Fraley *et al.*, 2012). Bayesian information criterion (BIC) is used to determine the best models and best number of classes based on the largest BIC value (Fraley *et al.*, 2012). We reran cluster solutions for all 20 classification scenarios and selected the best model for each scenario using the maximum BIC value.

Determining the explanatory power of various classification systems on spatial patterns can be confounded by spatial autocorrelation (i.e. the property where values in close spatial proximity are more similar than those located randomly). In addition, the degree of spatial autocorrelation may depend, in part, on spatial contiguity of given framework (i.e. the area defined by each region is consolidated by a discretely bounded space adjoining the next neighbouring regions); thus, biases attributed to spatial autocorrelative structure can be intensified in situations involving comparisons of spatially contiguous versus non-contiguous classifications (Wolock *et al.*, 2004; Frimpong and Angermeier, 2010a). For example, hydrologic classes are typically non-contiguous frameworks because single classes may be found in many separate discrete locations throughout the USA (Wolock *et al.*, 2004; Olden *et al.*, 2012). Ecoregions, on the other hand, are contiguous and confined to discrete bounded areas.

Several studies have applied approaches to explicitly account for spatial autocorrelation by creating null spatial

models to which a spatial classification is compared (Van Sickle and Hughes, 2000; Wolock *et al.*, 2004; Pyne *et al.*, 2007; Frimpong and Angermeier, 2010a). For example, Wolock *et al.* (2004) created square geometric regions, classes with no physical meaning, to approximate the same number of HLRs. Geometric regions were used as a baseline to assess the regionalization of environmental characteristics, i.e. variation explained solely by spatial autocorrelation. Hence, if HLRs explained more variation than the baseline, they were considered more effective than the null model. In this paper, we used spatial eigenvector filtering (Griffith and Peres-Neto, 2006), which provides for greater analytical flexibility than the null model approach. Spatial eigenvectors were derived from a spatial neighbourhood matrix of HUCs where HUC centroids separated by less than a given threshold distance were defined as neighbours. Using the centroids of each HUC-8, neighbourhood networks were constructed in the R programming environment (spdep package) under four distance thresholds: 100, 150, 200, and 500 km to visually determine an approximate optimal neighbourhood threshold, while ensuring that every HUC had at least one neighbour (Figure 3). We selected a neighbourhood threshold of 150 km because that provided each HUC-8 with at least one neighbour. The actual distance (d) was then weighted by the function $1-d_{ij}/\max(d_{ij})$, where d_{ij} is the distance between HUC_{*i*} and HUC_{*j*}. The weighted distances based on the maximum distance among all HUC-8 watersheds, with 0 values for non-neighbours, were then

used to calculate spatial eigenvectors. Positive eigenvectors exhibiting significant spatial autocorrelation were selected using a Moran's I test in R Principal Coordinates of Neighbour Matrices (PCNM package).

All 20 hydrologic classifications, ecoregions, HLRs, and provinces were summarized as the proportion of area within each HUC-8 (Figure 4). Significant eigenvectors were then used in logistic GLMs to predict the proportion of area within HUCs represented by each class, following Brind'Amour *et al.* (2011). Predicted values for each class were joined into a matrix of multivariate predictors, which were used to assess the strength for each classification system. Using multiple predictors for each classification system provided a mechanism to allow for more than one class to be represented within each HUC-8. Redundancy analysis (vegan package) in R was used to determine the amount of variation explained by each classification system (multivariate matrix) on life history strategies and then reproductive strategies. Redundancy analysis is advantageous in that multiple explanatory variables can be used to explain patterns in multiple response variables, such as trait values. In addition, redundancy provides a way to examine overlap in the variation explained by multiple predictors, such as multiple classes or even multiple classification systems. We compared R^2 values from hydrologic classes to all other classification systems. We then examined how combining the original 15 hydrologic classes with other classification systems influenced total variation, unique variation, and redundant variation (overlap).

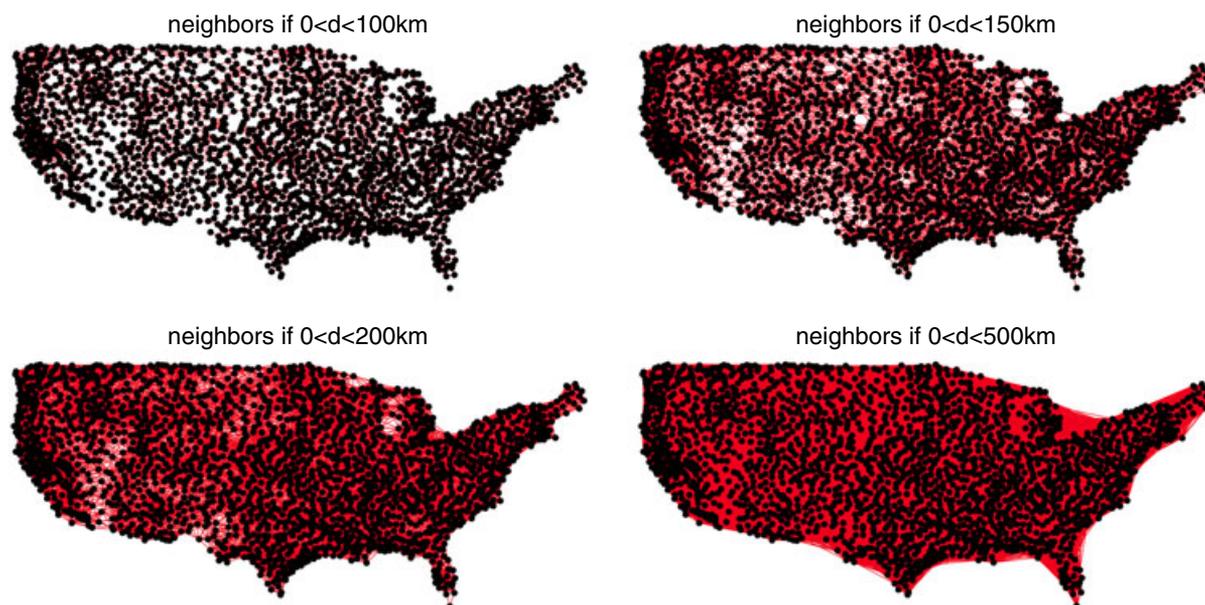


Figure 3. Spatial neighbourhood networks constructed using the centroids of hydrologic catalogue units under four distance thresholds: 100, 150, 200, and 500 km. Hydrologic catalogue units separated by 150 km or less were determined to be neighbours.

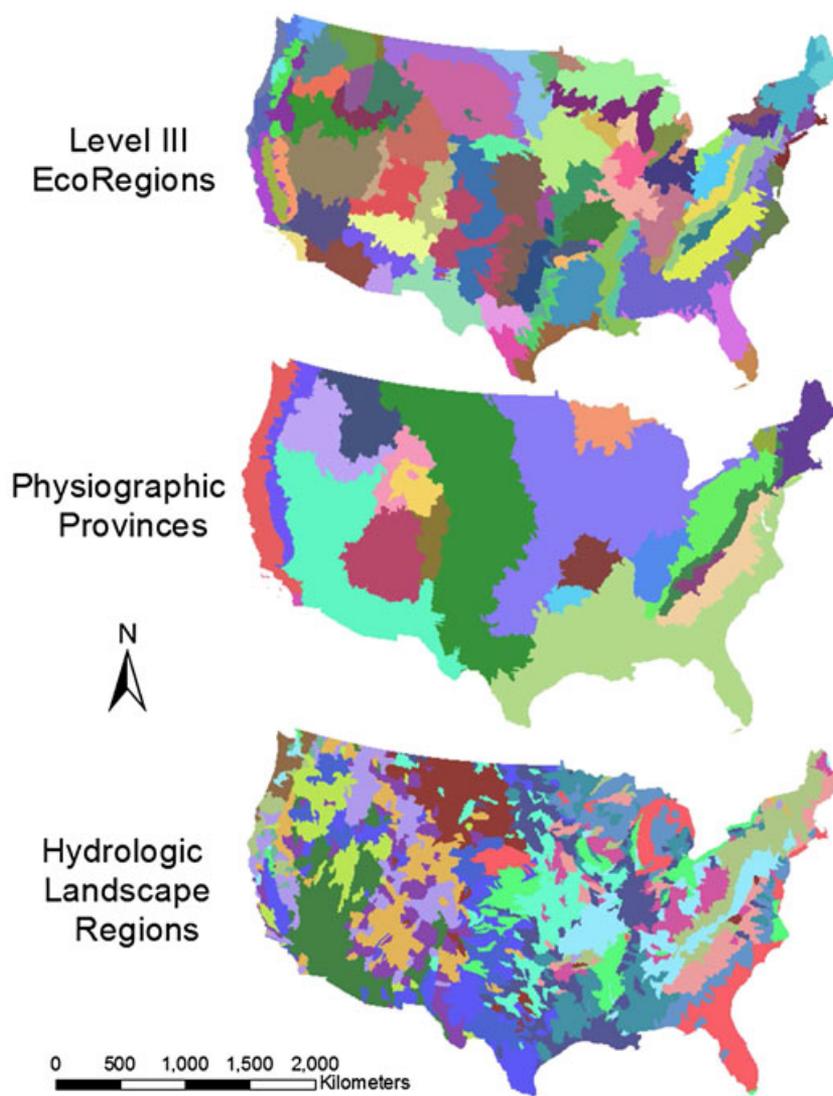


Figure 4. Dominant Level III Ecoregions, physiographic provinces, and Hydrologic Landscape Regions summarized within 8-digit hydrologic catalogue units in the conterminous USA.

RESULTS

Overview of fish traits and classification system information

We compiled trait information for 865 native freshwater fish species in North America. Family number had significant effects on fish traits in all generalized linear models except those for serial spawners and brood-hiders. On the basis of Euclidean distances of each species from the three life history groups' endpoints, 124 species were designated as periodic strategists, 303 as opportunistic strategists, and 303 as equilibrium strategists. Fish traits summarized for the entire HUC-8 assemblages displayed some geographical affiliation; however, similar values were also found in geographically separated areas (Figure 2).

All five classification systems were summarized for 2068 HUC-8 watersheds within the conterminous USA. For the hydrologic classification, 63% of HUC-8 watersheds had at

least 75% of their area comprised by a single dominant class. Only 31% of watersheds had only one hydrologic class represented (Supplementary Material 1). In comparison, at least 75% of watershed area was comprised by a single dominant EcoII, EcoIII, HLR, and province class in 83%, 71%, 34%, and 88% of watersheds, respectively (Supplementary Material 1). EcoII, EcoIII, HLRs, and provinces had a single class represented in 59%, 39%, 8%, and 72% of watersheds.

Multivariate trends in fish traits

Associations between hydrologic classes and fish traits were variable; however, patterns in fish traits were apparent when classes were sorted according to a spectrum of stable perennial flow to unstable intermittent flow (Figure 5). In general, opportunistic species, serial spawners, and summer spawners followed an increasing trend in classes displaying

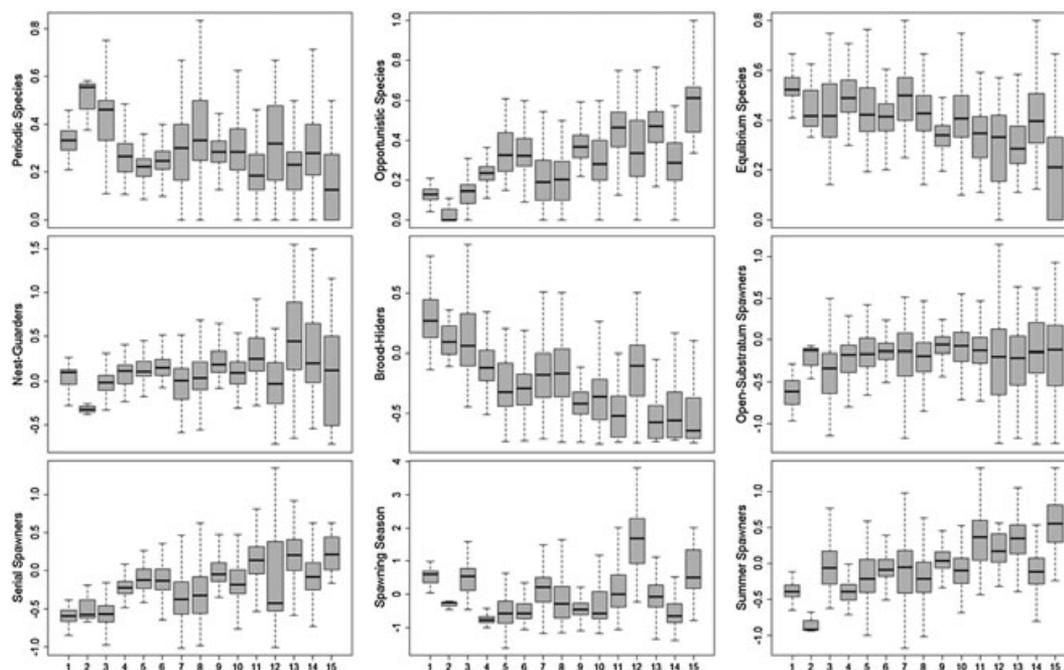


Figure 5. Box and Whisker plots of nine fish traits summarized within hydrologic classes. Classes were sorted from the highest to the lowest mean annual runoff ($\text{m}^3 \text{s}^{-1} \text{km}^{-2}$) from left to right. 1 = SHR, 2 = GHR, 3 = WCR, 4 = PR2, 5 = SHBF, 6 = PR1, 7 = SNM1, 8 = SNM2, 9 = UI, 10 = SSGW, 11 = LTR, 12 = IFSW, 13 = IF2, 14 = IF1, and 15 = HI. Class names are provided in Table I.

intermittency and lower mean annual runoff. In contrast, periodic species and brood-hiders tended to decrease with decreasing runoff and increasing intermittency.

Eigenvalues of the first three PCs exceeded those from random data (broken-stick model) and cumulatively explained 88% of the variation in fish reproductive strategies. Individually, PCs 1, 2, and 3 explained 60%, 18%, and 10% of the total variation, respectively. Fish assemblages displayed gradients of trait composition with contrasting reproductive strategies along opposite endpoints. Groupings according to hydrologic classes were apparent and showed signs of regional affiliation (Figure 6). For example, the largest variation in fish traits was associated with PC1, which corresponded to variation in spawning season length. Spawning season length was oriented along an east-to-west axis, with western hydrologic classes (SNM1-2, SHR, WCR, and IFSW) displaying longer spawning seasons (Figure 6). Brood-hiders and serial spawners were on opposite endpoints of PC2, whereas open-substratum and nest guardians were affiliated with opposite endpoints of PC3. Serial spawners and nest guardians were typically affiliated with intermittent flow classes, whereas brood-hiders and open-substratum spawning types showed strong associations with perennial flow types, especially in the western USA. Perennial runoff streams encompassed the centroid of fish trait multivariate space in both classification systems (Figure 6).

Fish assemblages also filled the entire trivariate life history space with some hydrologic classes displaying significant overlap (Figure 7). Fish assemblages within

intermittent classes tended to affiliate towards the opportunistic endpoint or along the axis connecting opportunistic and equilibrium endpoints (Figure 7). PR1-2, SHBF, SSGW, and UI streams tended to cluster in the centre of the space between the equilibrium and opportunistic endpoints, whereas SNM1-2, SHR, and WCR tended to cluster towards the axis connecting periodic and equilibrium species. LTR, SSGW, SNM1-2, and IF2 tended to occupy a larger trivariate space than the other classes (Figure 7).

All five components of the flow regime (magnitude, frequency, duration, rate of change, and timing) were represented by hydrologic indices with the strongest correlations with individual fish traits (Appendices 1 and 2). Fifteen of the hydrologic indices were represented, with 1-day high flow and fall rate being the most frequent followed by 3-day high flow, low-flow duration, and predictability (Appendices 1 and 2). Serial spawners, bearers, summer spawners, and opportunistic species were positively correlated with short-term high flows, daily CV, and rise/fall rates and negatively correlated with low-flow duration (Appendices 1 and 2). In contrast, equilibrium species and substrate choosers showed the exact opposite trends (Appendices 1 and 2). Spawning season and winter spawners were negatively correlated to low-flow and high-flow frequency. Spring and fall spawners were influenced by seasonal magnitudes, i.e. monthly flows.

Hydrologic and ecological distinction

Mahalanobis distances displayed varying degrees of hydrologic distinction among classes (Figure 8). Hydro-

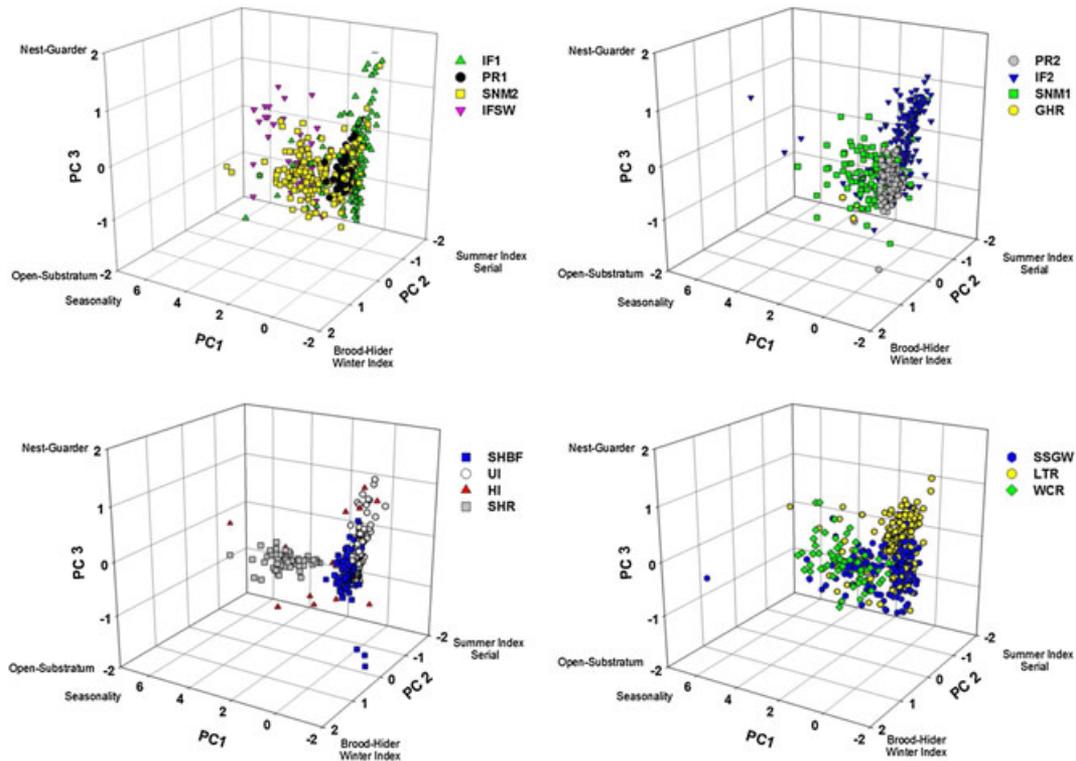


Figure 6. Multivariate distribution of reproductive strategies of fish assemblages along the first three principal components (PCs) according to hydrologic classes. Traits with the highest loadings are displayed along axes. Class names are provided in Table I.

logic distinction among classes was not driven by geographic separation as evidenced by the insignificant correlation between the hydrologic distinction matrix and geographic distance matrix (Mantel $r = -0.054$, $p = 0.593$). For example, SHBF streams were closely related to SNM2 and WCR streams despite occurring on opposite ends of the country. Typically, the hydrologic D^2 matrix displayed a spectrum of perennial and intermittent flows, with more intense intermittent streams being more hydrologically distinctive. In addition, fish trait distinction seemed to reflect hydrologic distinction, with more similar hydrologic classes sharing similar ecology (Figure 8). Fish trait distinction was positively correlated with geographic distance among hydrologic classes (Mantel $r = 0.444$, $p = 0.002$), and also positively correlated with hydrologic distinction (Mantel $r = 0.450$, $p = 0.013$). Because hydrologic distinction was not correlated with geography, the correlation between fish traits and hydrology was not based on geographic regionalization.

Classification strength

After re-running cluster analysis from 1 to 100 hydrologic classes, BIC maximized at 15 classes for the VEV model (ellipsoidal distribution, equal shape, and variable volume and orientation) as supported by McManamay *et al.* (2014) (Figure 9). For every fifth cluster solution (e.g. 5, 10, 15),

we selected the model with the highest local BIC value to produce 20 classification scenarios (Figure 9). From 1 to 40 clusters, the VEV model had the highest BIC values; however, for solutions >40 clusters, the VEI model (diagonal distribution, varying volume, and equal shape) had the highest BIC values (Figure 9).

Within the 150-km neighbourhood threshold among HUC-8 watersheds, 650 spatial eigenvectors were determined to display significant ($p < 0.05$) signs of spatial autocorrelation according to the Moran's I test. These 650 eigenvectors were then used to predict class membership for all HUC-8 watersheds for each classification system. Overall, the classification strength of hydrologic classes (R^2) was higher for reproductive strategies than life history groups, and in both cases, R^2 increased moderately with increasing numbers of classes (Figure 10). After accounting for spatial autocorrelation, hydrologic classes had consistently lower R^2 values than EcoII, EcoIII, and Provinces regardless of the number of classes (Figure 10). Hydrologic classes performed similarly to HLRs, having slightly higher R^2 than HLRs when explaining variation in life history groups and slightly lower R^2 than HLRs when explaining variation in reproductive strategies.

When hydrologic classes were combined with other classification systems, R^2 were higher if each classification system was considered separately (Table III). Results suggested, however, that redundancy in information was

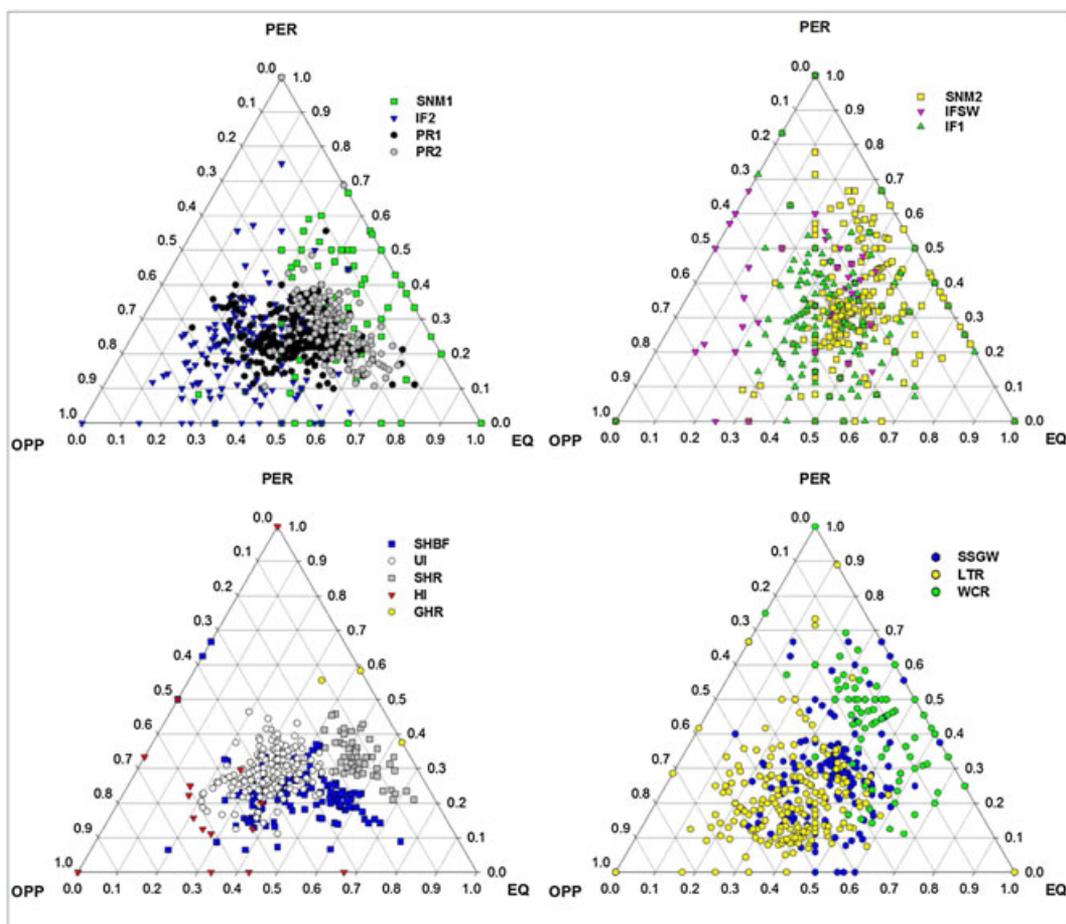


Figure 7. Ternary plots displaying the trivariate distribution of life history strategies of fish assemblages according to hydrologic classes.

prevalent between hydrologic classes and other classification systems. For example, variance explained by combining hydrologic classes with EcoIII was only slightly higher than R^2 for EcoIII separately. When hydrologic classes were combined with the remaining classification systems, increases in R^2 were more noticeable and comparable to variance explained by EcoIII (Table III).

DISCUSSION

We developed associations between two hydrologic classification systems and patterns of fish reproductive and life history traits as an initial step towards developing and testing a template for generating flow–ecology hypotheses and supporting environmental flow standard development. Associations between fish traits and individual hydrologic classes were evident, which could be used to infer class-specific flow–ecology hypotheses. Variation in life history and reproductive strategies across a gradient of stable, perennial flow to unstable intermittent flow, also suggested that fish life history traits vary predictably along gradients of hydrologic variability. Positive relationships

between hydrologic separation across flow classes and fish trait distinctiveness across flow classes provided additional evidence of coarse generalizable relationships between flow variability and ecological patterns at regional scales. These relationships between hydrologic and ecological class distinction may translate to testable predictions about the effects of losses in hydrologic distinctiveness and ecological community response. Ultimately, our results support the suggestion that environmental flow standards should be tailored towards distinctive individual stream flow classes and their distinctive ecological communities (Arthington *et al.*, 2006; Poff *et al.*, 2010).

Despite the evident patterns of association between hydrologic classes and fish traits, the ability of hydrologic classes to explain variation in fish traits was inferior to that of both Ecoregions and Provinces. On the basis of classification strength alone, it could be concluded that Ecoregions are superior to hydrologic classes in environmental flow management, despite the immense scientific justification for their creation and use (Arthington *et al.*, 2006; Poff *et al.*, 2010). However, as Wolock *et al.* (2004) suggested, the utility of any classification system is not necessarily related to its classification strength, especially if

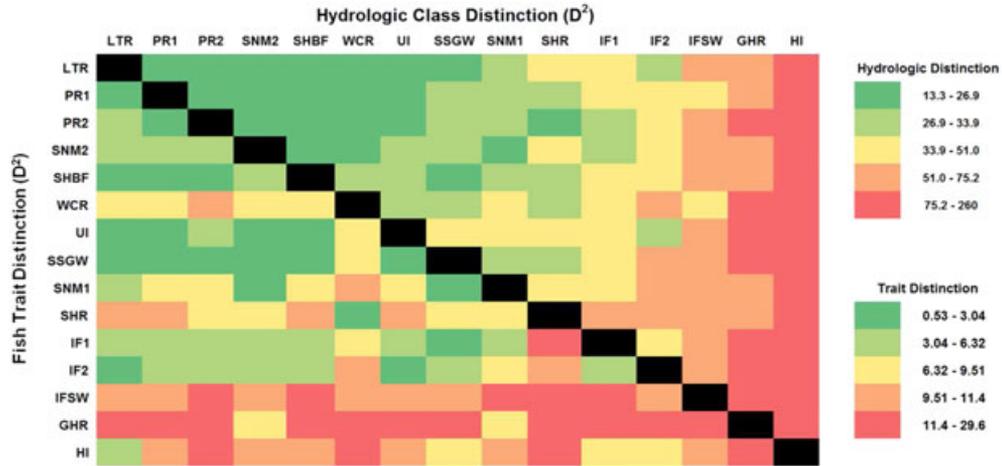


Figure 8. Comparison of distance (Mahalanobis D^2) matrices calculated for hydrologic classes on the basis of 36 hydrologic indices (top half matrix) and 14 fish traits summarized within classes (bottom half matrix). Matrices were sorted from left to right according to the smallest hydrologic distances. Class names are provided in Table I.

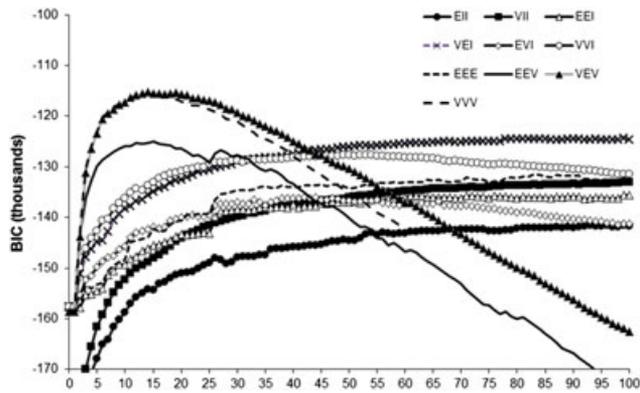


Figure 9. Bayesian information criteria (BIC) plots used to determine the best model for a given number of clusters, which occurs at the maximum BIC value. Star indicates the models and associated clusters with the highest BIC maximum value (VEV model, 15 clusters). Model names: spherical=EII (equal volume); VII (unequal volume); diagonal=EEI (equal volume, shape); VEI (varying volume, equal shape); EVI (equal volume, varying shape); VVI (varying volume, shape); ellipsoidal=EEE (equal volume, shape, orientation); EEV (equal volume, shape); VEV (equal shape); and VVV (varying volume, shape, orientation).

the underlying conceptual framework is missing, as in the case of geometric regions (i.e. null models). Furthermore, we suggest that classification strength is not synonymous with ecological relevance, at least in terms of advancing conceptual understanding. Unlike Ecoregions, hydrologic classes provide a conceptual linkage between hydrologic variation and the structure of ecological communities, specifically the trait composition of community members. Hence, the utility and success of hydrologic classification lie in their ability to provide a template for generating mechanistic flow–ecology hypotheses. In order to strike a balance between classification strength and a grounded conceptual basis, nesting hydrologic classes within other spatially contiguous frameworks, such as Physiographic

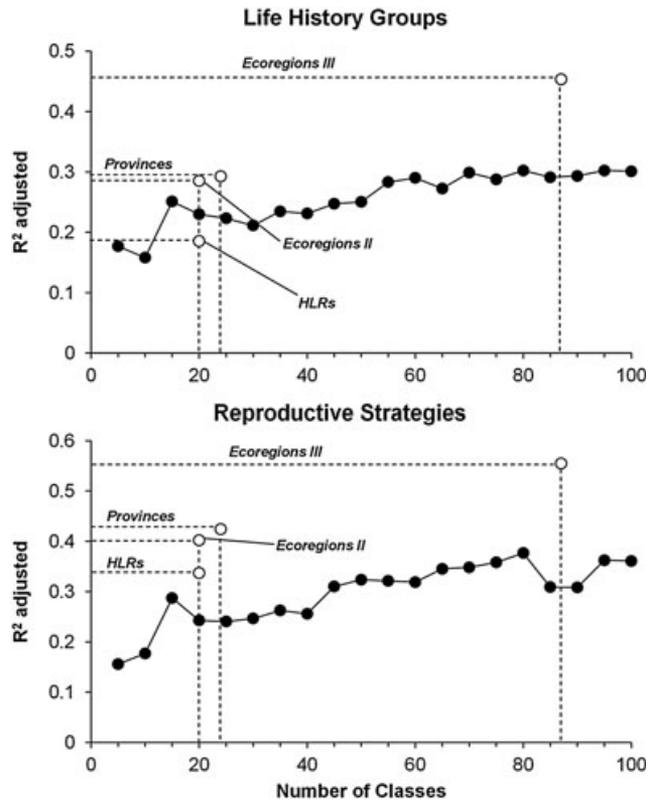


Figure 10. Comparison of classification strength (R^2) between hydrologic classes (black dots) and other classification systems (white dots) in explaining variation in fish life histories and reproductive strategies.

Provinces, may be the best approach (Frimpong and Angermeier, 2010a).

Hydrologic classes and fish traits

We observed patterns in fish traits suggesting adaptations in life history strategies along a gradient of perennial to

Table III. Comparisons of the classification strength (R^2) of four pre-existing classification systems relative to hydrologic classifications, independently and combined using redundancy analysis.

Classification system	df	Life history		Reproductive	
		Adj. R^2	Partial R^2	Adj. R^2	Partial R^2
Ecoregions III	87	0.45	0.22	0.55	0.28
Hydrologic class	15	0.25	0.02	0.29	0.02
Combined	102	0.47	0.23	0.57	0.27
Provinces	24	0.29	0.13	0.42	0.20
Hydrologic class	15	0.25	0.09	0.29	0.06
Combined	39	0.38	0.16	0.49	0.22
Ecoregions II	20	0.29	0.10	0.40	0.17
Hydrologic class	15	0.25	0.06	0.29	0.05
Combined	35	0.35	0.19	0.45	0.23
HLR	20	0.19	0.07	0.34	0.15
Hydrologic class	15	0.25	0.13	0.29	0.10
Combined	35	0.32	0.12	0.44	0.19

intermittent flow regardless of geographic affiliation. The importance of hydrologic variation and predictability in shaping fish assemblage structure has been well documented (Schlosser, 1987, 1990; Poff and Allan, 1995; Jackson *et al.*, 2001; Herbert and Gelwick, 2003; Pyron and Lauer, 2004). Hydrology forms the habitat template (Schlosser, 1987, 1990) or hierarchical filter (Jackson and Harvey, 1989; Tonn *et al.*, 1990; Poff, 1997), which underlies tradeoffs among biological traits and hence, predictable adaptive strategies among the members of fish assemblages. Southwood (1988) suggested that tradeoffs among the expression of various traits (i.e. tactics) produce suites of common life history strategies, some of which are favoured under various environmental conditions. For example, a small body size may be favoured in unpredictable environments because of energetic demands and space requirements; however, this likely occurs at the expense of lower fecundity (Winemiller and Rose, 1992). Because trait expressions and tradeoffs are physiologically constrained (Southwood, 1988) and repeated strategies emerge under common environmental pressures (Winemiller, 2005), reproductive and life history strategies provide a framework for predicting patterns in fish assemblages along hydrologic gradients.

Observed linkages among hydrologic classes and fish life history groups agree with the broader fish trait-hydrology conceptual framework proposed by Winemiller and Rose (1992) and expanded by Winemiller (2005). For example, under Winemiller's (2005) framework, periodic strategists have adapted to seasonally fluctuating, but predictable hydrology by attaining large sizes, taking longer to reach sexual maturity, having low parental investment, and requiring favourable conditions to spawn.

However, these strategies are adopted at the expense of low juvenile survivorship and poor recruitment when conditions are seasonally unpredictable. In general, we observed lower proportions of periodic strategists in the majority of intermittent stream classes and higher proportions in classes with strong seasonal components of perennial flow. Similarly, periodic strategists were more common in highly seasonal perennial rivers in the tropics of West Africa (Tedesco *et al.*, 2008). In contrast to periodic species, equilibrium strategists have low fecundity and high parental investment, but like periodic species, equilibrium species prefer predictable and stable perennial flows (Winemiller, 2005). Similar to periodic species, the proportion of equilibrium species tended to decrease with decreasing runoff. Tedesco *et al.* (2008) showed that stable drainage basins with extended wet seasons contained a higher proportion of equilibrium species.

Opportunistic strategists are short lived, have low parental investment, and may spawn several times within a year depending on conditions (Winemiller and Rose, 1992); thus, opportunistic species have the ability to inhabit harsh environments with unpredictable hydrology and recolonize rapidly following disturbances (Winemiller, 2005). Within our study, opportunistic species increased with increasing intermittency and decreasing flow predictability. Olden and Kennard (2010) found that within the USA and Australia, the proportion of opportunistic species increased with flow variability, whereas periodic species decreased as would be expected. Although Olden and Kennard (2010) found some similarities in their intercontinental comparison between the USA and Australia, distinctive qualities regarding fish traits also emerged suggesting a predominance of different hydrologic regimes. Compared with the USA, Australian fishes tended to predominately affiliate with the axis connecting opportunistic and periodic endpoints in multi-dimensional trait space, resulting in fewer species affiliated with the equilibrium strategy. The authors suggested that this intermediate strategy is adaptive in unpredictable and extreme harsh hydrologic contexts marked occasionally by complete recruitment failures. Intercontinental differences in fish traits are likely the result of predominant differences in the hydrologic character between the USA and Australia. For example, in a continental hydrologic classification for Australia, eight of the 12 hydrologic classes were considered intermittent types (Kennard *et al.*, 2010b) compared with only five out of 15 hydrologic classes for the US classification.

Reproductive strategies also showed some patterns among hydrologic groups; however, there was considerable variation, primarily due to region affiliation. Brood-hiders were negatively associated with intermittency; however, the largest positive values were associated with Western classes containing a higher proportion of salmonids (SNM

streams – reference; SHR, GHR, WCR – expanded). Species displaying varying degrees of parental care (bearers, nest guards, and substrate choosers) showed little response to hydrologic variation. Typically, species displaying more parental care (i.e. equilibrium species) are considered to prefer stable and predictable environments (Winemiller, 2005). For example, equilibrium species may be more common in the USA compared with Australia because of more predictable flow environments (Olden and Kennard, 2010). However, Carlisle *et al.* (2011) found that nest guards increased in streams with deflated minimum flows (i.e. less stability). Nest guarding behaviour, and increased parental care in general, may be advantageous in some circumstances because optimal nest habitat can be selected in areas protected from abrupt changes in stage or flashy high flows. Open-substratum spawners, on the other hand, have little parental investment and deposit eggs on the surface of substrates; thus, eggs may be susceptible to hydrologic events that disturb substrates. For example, Craven *et al.* (2010) found that broadcast spawners (low parental investment) were negatively influenced by high-magnitude, short-term flow events compared with other reproductive strategies because eggs are susceptible to substrate disturbance. Carlisle *et al.* (2011) showed that broadcast spawners increased in streams with decreased maximum flow, suggesting that substrate stabilization may induce conditions favourable to low parental investment. However, responses by open-substratum (i.e. broadcast) spawners in our study were highly variable across classes and not negatively associated with classes displaying increased high-flow frequencies or magnitude. Thus, in order to elucidate trends in reproductive strategies, localized information specific to individual systems (e.g. substrate conditions) may be required.

Although patterns in fish traits were evident along a gradient of perennial flow, there was considerable variability in fish traits suggesting that other hydrologic or non-hydrologic variables were at play. For example, higher runoff estimates for some classes do not necessarily imply consistent perennial flow (e.g. UI1, reference set). Spawning season traits, such as timing of spawning and season length, showed more affiliation to regions than hydrologic variation. Hydrologic classes in the western USA (SNM1-2, CHR, SHR, and WCR) had higher winter and fall spawning indices, whereas classes in the eastern USA (SHBF, PR1-2, UI) showed lower values for winter and fall spawning. Craven *et al.* (2010) suggested that spawners with longer spawning seasons would be less susceptible to short-term disturbance floods, which are common in intermittent-type systems. Intermittent classes, however, displayed no apparent patterns in spawning season preference or season length.

Hydrologic and ecologic distinction

Because the natural flow regime is a multivariate concept (Poff *et al.*, 1997), discerning patterns in flow–ecology relationships may require considering multiple dimensions. We observed strong positive correlations between hydrologic class distinction and fish trait distinction and between geographic distance and fish trait distinction. However, we also observed an insignificant correlation between hydrologic distinction and geographic separation, which suggested that hydrologic variation is not necessarily driven by geographic separation. For example, SHBF streams shared similar hydrologic patterns to SNM2 and WCR streams despite being geographically closer to PR1, PR2, and UI streams. Hence, the strong correlation between hydrologic distinction and fish trait distinction was not an artefact of geography.

Incorporating ecological discriminatory capacity in the environmental classification process is a robust approach to providing the most ecologically relevant solution (Leathwick *et al.*, 2011). Environmental variables that best explained biologic dissimilarities were used as ecologically relevant input for multivariate classification of river segment habitats in New Zealand (Leathwick *et al.*, 2011). In other words, biological data can be used to inform the clustering process *a priori*. Indeed, both Arthington *et al.* (2006) and Poff *et al.* (2010) stressed using ecologically relevant flow variables in hydrologic classifications. Our approach differed to that of Leathwick *et al.* (2011) in that comparisons of clustering solutions to biological data are conducted post hoc and all environmental predictors (i.e. hydrologic indices) are incorporated. In either case, tradeoffs among classification complexity (i.e. number of clusters) and biological discriminatory power can be balanced in favour of the most parsimonious solution.

Assessing commonalities between class distinction and ecological responses aids in not only refining classification solutions but also developing generalities for environmental flow management. For example, in light of hydrologic disturbances, rather than rely solely on univariate hydrologic-ecologic response curves to anthropogenic changes, changes in class membership or losses in hydrologic uniqueness may isolate more meaningful relationships (Rolls and Arthington, 2014). Richter (2010) suggests that flow standards be based on thresholds, which once surpassed, begin compromising ecological goods and services. Because of the multivariate nature of flow regimes, potential hydrologic thresholds could be viewed as changes in class memberships (e.g. streams of a particular class function more like a different hydrologic class following alterations in flow regimes). If a strict interpretation of the natural flow regime is taken, then a river's flow regime should be assessed and

managed as a multivariate sphere where hydrologic disturbances and ecological responses can be measured in terms of distance from multivariate centroids and outliers.

Classification strength

Ultimately, we found that hydrologic classes explained less variation in fish traits than Ecoregions and provinces, before and after accounting for spatial autocorrelation. The strength of classification systems is related to ecological relevance, and also the number of classes, spatial autocorrelation, and spatial contiguity. After evaluating the amount of variation in fish traits explained by multiple individual classification systems, Frimpong and Angermeier (2010a) concluded that classification strength was positively related to the number of classes and spatial autocorrelation, as evidenced by Ecoregions explaining the most variation, followed by provinces, and then HLRs. We observed, however, that after increasing the number of hydrologic classes and incorporating spatial autocorrelative data structure in each classification, hydrologic classes still had lower classification strength than Ecoregions and Provinces.

Spatially contiguous frameworks, such as Ecoregions and Provinces, have been described as having high regionalization power (Wolock *et al.*, 2004) because each region is consolidated to one area and most ecological data are also spatially autocorrelated (Frimpong and Angermeier, 2010a). Spatially contiguous frameworks typically outperform non-contiguous frameworks when explaining variation in autocorrelated data structure, because spatial consolidation is synonymous with consolidating variation. In contrast to Ecoregions and Provinces, hydrologic classifications, like HLRs, are spatially discontinuous, i.e. classes can be found in multiple discrete locations across the USA. Because of biases associated with spatial contiguity, null spatial models have been used to account for or spatial autocorrelation induced by regionalization (Van Sickle and Hughes, 2000; Wolock *et al.*, 2004; Pyne *et al.*, 2007; Frimpong and Angermeier, 2010a). Wolock *et al.* (2004) found that, in some cases, square geometric regions, i.e. null models, explained as much or more variation in environmental variables than HLRs. Likewise, Frimpong and Angermeier (2010a) showed that relative to the number of classes, neutral grids explained more variation in fish traits than HLRs and less variation than Ecoregions, Zoogeographic Regions, and Provinces. These findings suggest that regions without any conceptual linkage to ecological patterns can have as high or higher classification strength than meaningful classification systems (Wolock *et al.*, 2004).

Given that ecological community data show strong patterns in regionalization and spatial autocorrelation,

nesting spatially discontinuous classes within contiguous classification systems may provide higher classification strength while also retaining the conceptual basis of the original framework. For example, Frimpong and Angermeier (2010a) explored nesting HLRs within zoogeographic regions, Ecoregions, and physiographic provinces resulting in higher variation explained in fish traits. The study concluded that despite explaining insignificant patterns as a stand-alone framework, HLRs are a useful concept if nested within regions. Likewise, we found that hydrologic classes, when combined within other frameworks, explained more variation than other classification systems in isolation. We suggest using hydrologic classes nested within Provinces or EcoII regions to increase classification strength while also providing a manageable number of classes with mechanistic linkages between hydrology and ecology.

Limitations of applying classes to the landscape

Ideally, the resolution of biological data used to test the predictive capacity of a given classification system should be consistent with that of the classification. The two main limitations of our analysis related to spatial resolution included (1) the assignment of hydrologic classes to the landscape via HUC-8 and (2) using fish species per HUC-8 rather than the more detailed river segment data. Applying hydrologic classes to HUC-8 watersheds on the basis of solely on gauge location may have masked important hydrologic variation at smaller scales. Olden *et al.* (2012) indicate that streams within the same region are not necessarily hydrologically homogenous and substantial spatial overlap exists among hydrologic classes. We addressed this issue by allowing every hydrologic class present to contribute as area-weighted proportions to HUC-8 watersheds. In addition, redundancy analysis is flexible in that it allowed for all 15 hydrologic classes to contribute as predictors for fish trait composition within each HUC-8.

The second potential discrepancy with our methods was that the use of coarser resolution biological data would lead to lower explanatory power as opposed to using reach-specific data [e.g. U.S. Geological Survey National Water-Quality Assessment (NAWQA) Program]. Frimpong and Angermeier (2010a) used fish sampling information from 1166 NAWQA sites to compare the ability of classification systems, including those in this study, to explain variation in fish traits. Percent of variation reported was 1–30% in their study compared with 19–57% in the current study. A major part of our reasoning in assigning classes to HUC-8 boundaries was twofold. First, we preferred the comprehensive and spatially contiguous list of all species occurrences, current and historical, within each HUC-8 across the conterminous USA. In comparison, the majority of ‘reference’ sites within discrete bio-monitoring data-

bases, such as NAWQA, represent small-medium size streams and only current species accounts; thus, they may not represent the variability of fish traits influenced by hydrology at large scales and may exclude larger river species. Second, at the reach scale, factors such as temperature, sediment, and geomorphology, exert localized controls on fish assemblages and must be accounted for in analyses. At the watershed scale (HUC-8), localized factors are arguably less important than hydrologic drivers in determining ecological patterns (Jackson *et al.*, 2001).

CONCLUSIONS

Hypothesis generation is among the most important products of classification systems (Sokal, 1974). Herein, we linked large-scale patterns in fish assemblages to hydrology, which provides a template to create and test hypotheses regarding flow–ecological response relationships. Prior to developing and testing univariate flow–ecology relationships within hydrologic classes, a robust approach would be to ascertain how ecological patterns (or processes) differ among classes and the specific role of hydrology in discriminating ecological patterns (Rolls and Arthington, 2014). The full potential of hydrologic classes in water and environmental flow management is that they define the unique multivariate correlates of stream ecosystem structure/function; thus, they can be used in predicting how disturbances (such as flow regulation) may create conditions that are more similar or more different to other classes, and accordingly generate different ecological patterns. For example, Rolls and Arthington (2014) evaluated how hydrologic alterations from dam regulation may affect fish assemblages differently depending on hydrologic class membership. As another example, Reidy Liermann *et al.* (2012) showed that following a climate change scenario, dominant hydrologic class membership shifted from snowmelt systems to rain-dominated classes. The key hydrologic and ecological elements important in discriminating stream classes can then be used to inform development and testing of flow alteration–ecological response relationships (Poff *et al.*, 2010). A robust alternative to conducting post hoc assessments of ecological distinction among classes is to incorporate ecological discriminatory power as part of the classification process (Leathwick *et al.*, 2011), thereby simultaneously gaining insight into hydrologic variable importance and ecological relevance.

In cases of comparing the ecological relevance of classification systems, we urge caution when concluding that lower classification strength necessarily suggests poorer utility. The basis of classification systems is to describe the current state of knowledge within a given discipline (Melles *et al.*, 2012) and provide a theoretical foundation from which hypotheses are created and tested (Sokal, 1974). Hydrologic classifications provide a multi-

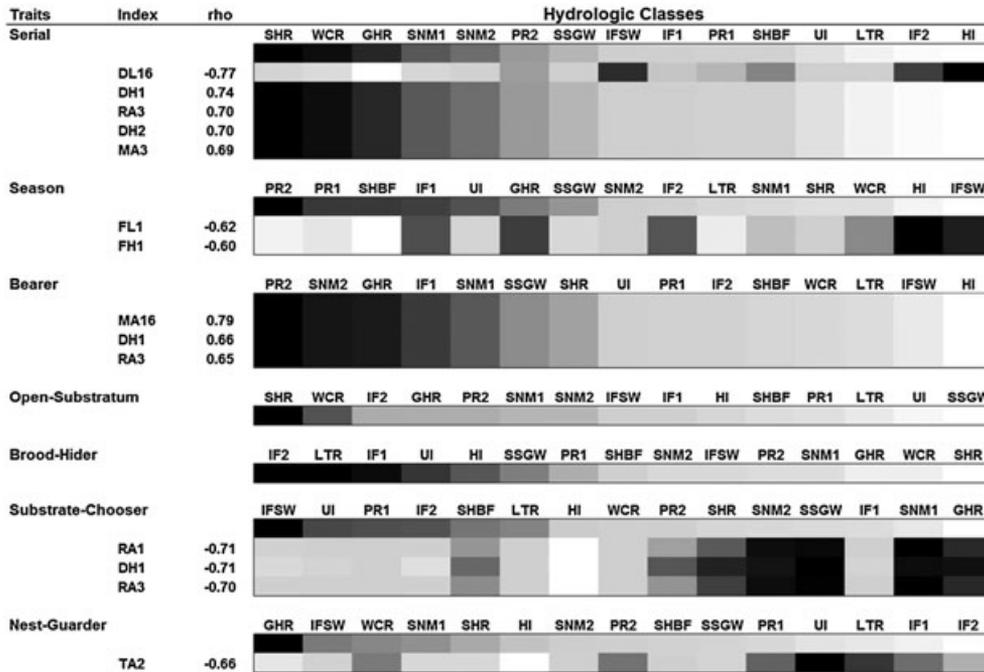
variate template for development of testable hypotheses expressing relationships between patterns of flow variability and ecological adaptations to inform environmental flow management. Although the general idea of incorporating river classification and associated ecological relationships into environmental flow management and policy has been proposed (Arthington *et al.*, 2006) and expanded (Poff *et al.*, 2010), the full potential of hydrologic classification systems has not been realized. Linkages between classes and specific ecological patterns must be established in a multivariate template (Rolls and Arthington, 2014). We have provided an example of how hydrologic and ecological uniqueness can be assessed, which provides a foundation for proposing and testing generalized ecological responses to losses in uniqueness or changes in class membership. In addition, the approach can be adapted to generalize how specific disturbances may alter the multivariate nature of flow regimes, create outliers, and then drive systems into altered ecological states (Rolls and Arthington, 2014). This approach supports the development of environmental flow standards by determining multivariate flow regime thresholds or sustainability boundaries (Richter, 2010).

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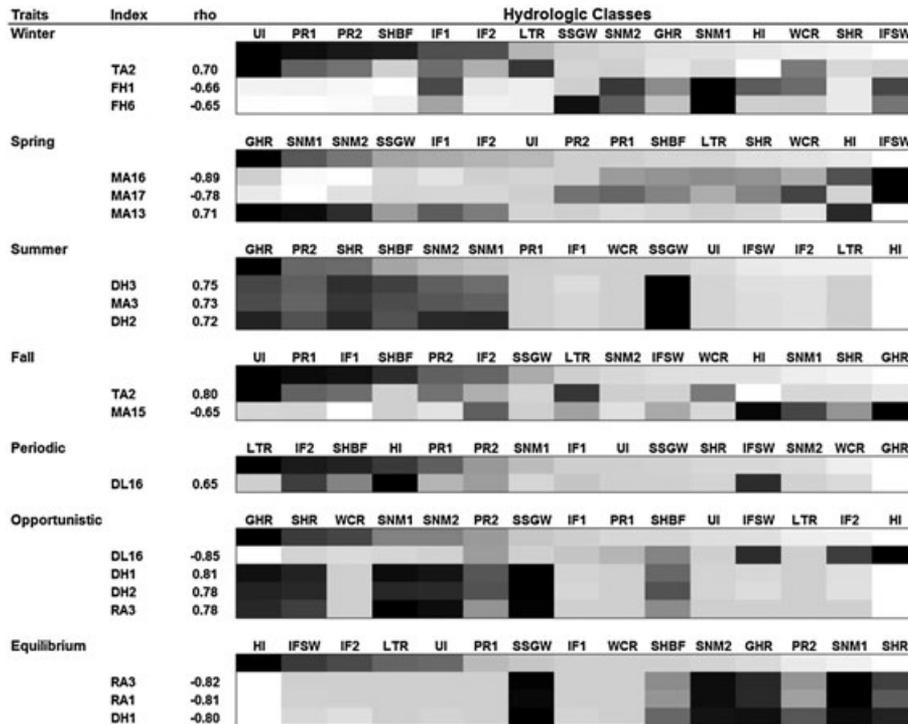
APPENDIX A

Correlogram depicting correlations between trait values and hydrologic indices across hydrologic classes. Classes were sorted from the lowest (black) to the highest (white) trait values. Hydrologic indices with the highest correlations (ρ values >0.6) for each trait were included and sorted on the basis of trait values.



APPENDIX B

Correlogram continued.



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