Relating Streamflow Characteristics to Specialized Insectivores in the Tennessee River Valley: A Regional Approach

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Abstract

Analysis of hydrologic time series and fish community data across the Tennessee River Valley identified three hydrologic metrics essential to habitat suitability and food availability for insectivorous fish communities in streams of the Tennessee River Valley: constancy (flow stability or temporal invariance), frequency of moderate flooding (frequency of habitat disturbance), and rate of streamflow recession. Initial datasets included 1,100 fish community sites and 300 streamgages. Reduction of these datasets to sites with coexisting data yielded 33 sites with streamflow and fish community data for analysis. Identification of critical hydrologic metrics was completed using a multivariate correlation procedure that maximizes the rank correlation between the hydrologic metrics and fish community resemblance matrices. Quantile regression was used to define thresholds of potential ranges of insectivore scores for given values of the hydrologic metrics. Increased values of constancy and insectivore scores were positively correlated. Constancy of streamflow maintains wetted perimeter, which is important for providing habitat for fish spawning and increased surface area for invertebrate colonization and reproduction. Site scores for insectivorous fish increased as the frequency of moderate flooding (3 times the median annual streamflow) decreased, suggesting that insectivorous fish communities respond positively to less frequent disturbance and a more stable habitat. Increased streamflow recession rates were associated with decreased insectivore scores. Increased streamflow recession can strand fish in pools and other areas that are disconnected from flowing water and remove invertebrates as food sources that were suspended during high-streamflow events.

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Introduction

Streamflow is a crucial determinant of the structure, composition, and health of riverine ecosystems. Numerous studies have been published describing the relation between streamflow regimes to riverine ecosystems over the past 50 years. Westgate (1958), Rantz (1964), Hoppe and Finnell (1970), and Tenant (1976) provided some of the first evidence that linkages between streamflow and aquatic community response could be determined and that perturbation of a flow regime (of a discharge time series or hydrograph) could elicit a response in the aquatic community. The results of these studies provided a foundational knowledge of the functional relations between hydrologic metrics and the aquatic community. With the notable exception of Tenant (1976), these early studies were generally conducted on single rivers. Together, they produced hydrologic metrics and conceptual understandings that began the advancement of environmental flow science. Nearly 50 years later, significant advances in research from a broad international community continue to be aimed at determining specific measures of flow regimes that, when altered, cause a change in a given riverine ecosystem, with the scope of these studies having become increasingly regional in scale (Westgate, 1958; Rantz, 1963; Hoppe and Finnell, 1970; Tenant, 1976; Hughes and James, 1989; Poff and Ward, 1989; Richards, 1989, 1990; Peterson and Stevenson, 1992; Poff and Allan, 1995; Clausen and Biggs, 1997, 2000; Puckridge and others, 1998; Richter and others, 1998; Clausen and others, 2000; Wood and others, 2000; Bertrand and others, 2001; Freeman and others, 2001, 2007; Freeman and Marcinek, 2006; Krstolic and others, 2006; Monk and others, 2007; Konrad and others, 2008).

Resource managers face the challenge of developing water management plans that meet multiple, sometimes conflicting, demands, one of which includes maintaining riverine ecosystem integrity. Awareness of the important function of flow regimes and flow-regime alteration to the structure and composition of fish communities has increased parallel to research into environmental flow needs (Westgate, 1958;

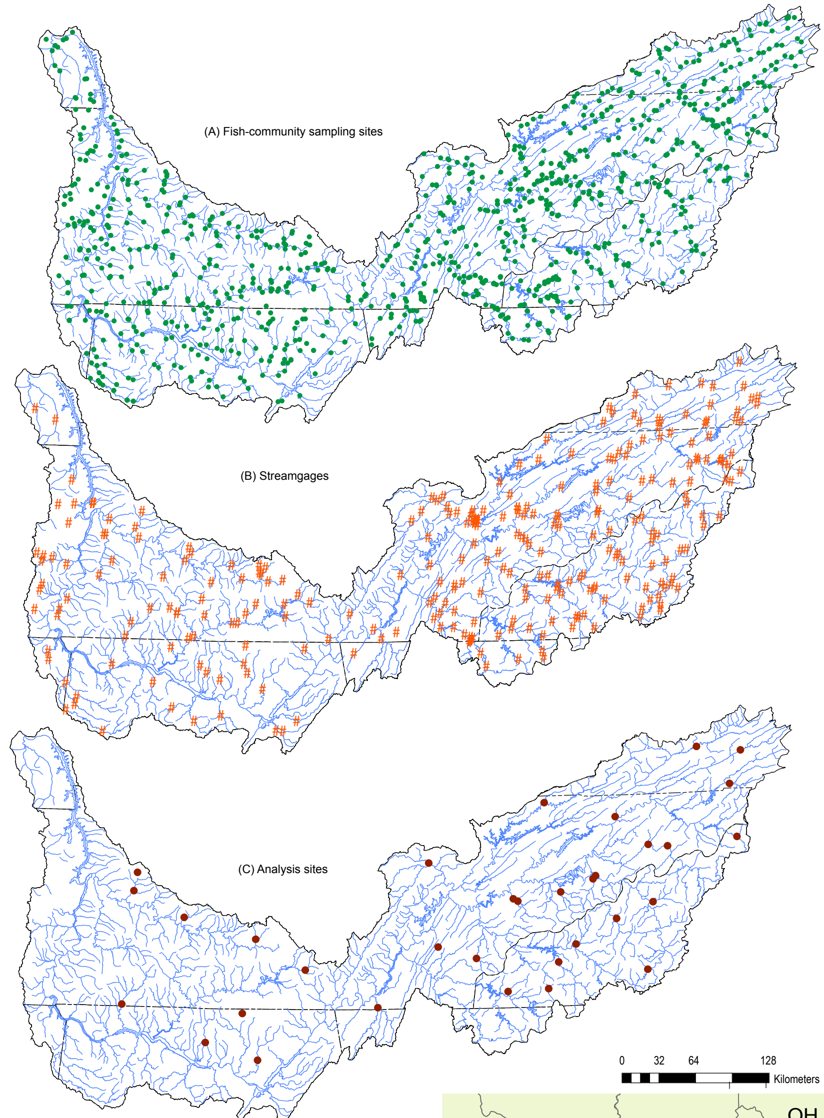
Rantz, 1963; Hoppe and Finnell, 1970; Tenant, 1976; Hughes and James, 1989; Poff and Ward, 1989; Richards, 1989, 1990; Peterson and Stevenson, 1992; Poff and Allan, 1995; Clausen and Biggs, 1997, 2000; Puckridge and others, 1998; Richter and others, 1998; Clausen and others, 2000; Wood and others, 2000; Bertrand and others, 2001; Freeman and others, 2001, 2007; Arthington and others, 2006; Freeman and Marcinek, 2006; Krstolic and others, 2006; Monk and others, 2007; Konrad and others, 2008). Leopold (1960) discussed the need to develop a scientific reference condition or period to understand how natural resources, including hydrology and ecology, were changing as the result of human activities. Richter and others (1996) and The Nature Conservancy (2007) proposed a suite of hydrologic parameters that can be used to quantify the degree of modification to flow regimes resulting from different scenarios using ecologically relevant indices. The Heinz Center (2006, 2008) has proposed core national indicators of streamflow change linked to changes to the Nation's ecosystems. The National Fish Habitat Action Plan (2006, 2007) identified restoration of natural streamflow variability as an important national strategy for maintaining fish habitat. The importance of environmental flow science has risen to such a level that in 1998 the Instream Flow Council was created. The Instream Flow Council aims to improve the effectiveness of environmental flow programs at protecting, maintaining, and restoring aquatic ecosystems (*http://www.instreamflowcouncil.org*). Currently, hydrologic metrics that have not been related to a particular faunal group are used to protect riverine ecosystem health. Examples include specific low-flow duration and frequency values, annual or monthly low-flow values, or watershed yield used for water supply or waste assimilation needs (Lang, 1999; Georgia Environmental Protection Division, 2001; Maine Department of Environmental Protection, 2007). Ecologically relevant hydrologic metrics that can be regionally applied are needed so that regulatory agencies can administer consistent and relevant rules for permitting streamflow modification (Arthington and others, 2006).

Research into environmental flow requirements is no longer limited by inadequate streamflow and ecology datasets for analysis. Within the United States alone, there are more than 25,000 stream sites with continuous streamflow data available from the U.S. Geological Survey (*http://nwis.waterdata.usgs.gov/nwis/sw*). Streamflow databases and metrics can now be assembled, calculated, and incorporated into research efforts with minimal effort. New tools such as the Indicators of Hydrologic Alteration by The Nature Conservancy (2007) and the Hydrologic Integrity Tool (Henriksen and others, 2006) allow ecologically relevant hydrologic metrics to be easily calculated and incorporated in studies. These include metrics and concepts identified by research using periphyton (Peterson and Stevenson, 1992; Clausen and Biggs, 1997, 2000; Clausen and others, 2000; Bertrand and others, 2001), invertebrates (Wood and others, 2000; Monk and others, 2007), fish (Poff and Allan, 1995; Puckridge and others, 1998; Freeman and Marcinek, 2006; Krstolic and others, 2006), general lotic community structure and variability (Hughes and James, 1989; Poff and Ward, 1989; Richter and others, 1998), and streamflow variability (Richards, 1989, 1990; Richter and others, 1996, 1997).

Given the existing streamflow network, the major limitation on regional analyses of the interaction between streamflow regime and riverine ecosystems has been availability of biological data. Progressive development of state and regional databases of aquatic biota *http://www.dep.state.fl.us/labs/cgi-bin/sbio/database.asp*; Cuffney, 2003) over the past several decades offers ample potential for new approaches to quantifying this interaction. A first step to such quantification is statistical analysis to identify streamflow characteristics that can be related to specific components of riverine ecosystems. This paper presents an example of an exploratory analysis using fish community data from the Tennessee River Valley.

Study Area

The Tennessee River Valley encompasses approximately 106,200 square kilometers and is home to at least 230 species of fish, 141 freshwater mussels, 160 aquatic snails, 115 crayfish, and North America's largest salamander, the hellbender (*Cryptobranchus alleganiensis*). The physiography of the Tennessee River Valley is similarly diverse. The sites used in the analysis for this study were located in four Level 3 ecoregions—the Blue Ridge, Ridge and Valley; South-west Appalachians; and Interior Plateau, although the South-west Appalachians represents only 13% of the total area. The three primary ecoregions—the Blue Ridge, Ridge and Valley, and Interior Plateau—are diverse in regard to physiohydrographic factors. The Blue Ridge ecoregion has thick soils and streams with steep gradients and predominately gravel/cobble substrate. Streamflow is typically sustained during dry periods of the year by groundwater discharge augmented by limited snowmelt at high elevations. The Interior Plateau has two subregions with distinct physiohydrography: the Highland Rim and the centrally located Nashville/Bluegrass Basins (Fenneman, 1938). The Interior Plateau in the Nashville/Bluegrass Basins has well-developed karst terrain with thin soils and low-gradient streams with bedrock substrate covered by thin gravel deposits in some areas (Burchett, 1977). Groundwater discharge is limited because of shallow soils and karst geology, allowing for quick movement of water out of storage. Typically, base flow in the Nashville/Bluegrass Basins streams significantly diminishes by mid-summer compared to streams in the Highland Rim. Highland Rim watersheds have thicker soils and streams with thicker gravel/cobble substrate relative to the Nashville/Bluegrass Basins. Ridge and Valley watersheds are characterized by shallower soils and lower gradients than Blue Ridge watersheds. The substrate in Ridge and Valley streams usually consist of a mixture of cobble and gravel with some exposed bedrock. Groundwater contributions to streamflow in the Ridge and Valley are generally greater than in Interior Plateau sites and result from water storage capacity



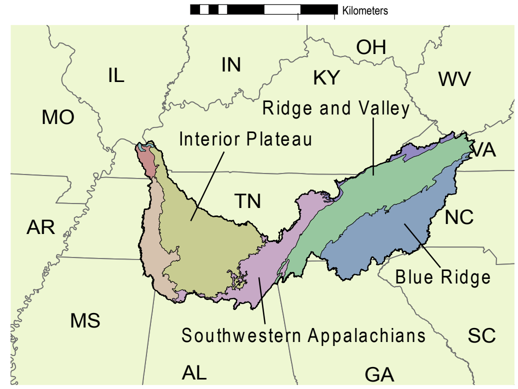


Figure 1. Distribution of (A) Tennessee Valley Authority fish sampling sites, (B) U.S. Geological Survey streamgages with continuous streamflow records, and (C) sites where fish-community and streamflow data were collected in the vicinity of each other in the Tennessee River Valley, 2000 - 2005.

of thicker soils and less karst development. Karst development can, however, be extensive locally in the Ridge and Valley (Bailey and Lee, 1991).

Temperature and precipitation in the Tennessee River Valley vary with longitude and elevation. Average annual temperature in the area is 13.9 ºC, while average annual temperatures across the area range from 11.1 ºC in the northern Blue Ridge ecoregion to 14.4 ºC in the Interior Plateau. The warmest months of the year are July and August, and the coldest months of the year are typically January and February (U.S. Department of Commerce, 2007a). The Interior Plateau averages about 1,400 mm of precipitation annually, compared with 1,350 mm in the Blue Ridge ecoregion and 1,450 mm in the Southwestern Appalachians and Ridge and Valley ecoregions (U.S. Department of Commerce, 2007b). Locally, precipitation amounts in the Blue Ridge can exceed 2,000 mm annually at the exposed balds and peaks at higher elevations of the Great Smoky Mountains National Park in East Tennessee and western North Carolina.

Methods

Data collection and computations

Fish community data from the Tennessee Valley Authority (TVA) were used in this study because of the large number of sites sampled (approximately 1,100 sites sampled one time) (Figure 1a), the large spatial area sampled (106,200 square kilometers), and the consistent use of sampling protocols by the U.S. Geological Survey National Water-Quality Assessment (NAWQA) Program (Moulton and others, 2002) and TVA (Tennessee Valley Authority, 1997). Sample data included the index of biotic integrity (IBI) score and component metrics as well as the community information such as the total number of species, number of individuals, and species present. Fish community data used in the analysis were collected between 2000 and 2005, representing one complete cycle of sampling by TVA with the single objective of calculating the IBI and component metric scores. Additionally, fish community sampling was done during the spring and summer months, primarily June and July for this study. Sampling during the spring and summer reduces the number of young-of-year fish in the sample. Sampling beyond this period increases the difficulty in differentiating young-of-year from adult fish. Young-of-year fish are not included in the IBI analysis because they have not been subjected to site conditions long enough to fully reflect those conditions and may artificially affect the score. Additionally, sampling during this period avoids the decreasing water temperatures of fall and winter that cause some fish to go into hiding and be difficult to capture. Fish community samples were collected using a habitat depletion method. With this method, each habitat present in the stream (riffle, run, pool, and shoreline) was sampled three times typically using backpack electroshocking equipment. The habitat type was considered depleted after three passes over a given habitat type without a new species. If a new species was collected, three additional passes were completed until no new species were found. The use of backpack electroshocking equipment dictated that streams be wadable as well as clear enough, so that fish could be seen and collected. Nonnative fish species were removed from the dataset, leaving 127 native fish species in the analysis. Site richness ranged from 10 to 58 (mean 32) and absolute abundances at each site ranged from 146 to 3,856 individuals (mean 1,335).

Streamflow data have been collected by various State and Federal agencies, especially the U.S. Geological Survey, throughout the study area. Requirements for including hydrologic data were that daily mean discharge be collected and processed using consistent methods (Rantz, 1982) and be digitally available. Hydrologic time series for more than 300 streamgages located across the Tennessee River Valley were retrieved from the U.S. Geological Survey's National Water Information System (NWIS) (*http://waterdata.usgs.gov*) (Figure 1b). These streamgages represent 300 potential sites for use in analysis.

Hydrologic metrics, including traditional descriptive and ecologically relevant streamflow characteristics, were calculated using daily mean streamflow records. Traditional descriptive characteristics for each site included 30 statistics describing low-flow values (7Q10, for example), frequency of flow events (50-year flood, for example), duration (percentiles), and general magnitude values (mean annual flow and watershed yield, for example).

Additional streamflow characteristics considered to be ecologically relevant were also included in the hydrologic-metric dataset. There are more than 200 such metrics according to Monk and others (2006, 2007), though some are redundant in the streamflow characteristic they describe. Olden and Poff (2003) describe this redundancy and provide metrics describing particular streamflow regimes for streams in the Tennessee River Valley (Olden and Poff, 2003—Table II, superstable/stable groundwater and perennially flashy/runoff streams). Sixty hydrologic indices identified by Olden and Poff (2003) and subsequently incorporated into software applications (Henriksen and others, 2006) were used in this analysis. These parameters represent critical components of the flow regime (Richter and others, 1996; Poff and others, 1997) and quantify low, average, and high flows within five flow-regime categories: magnitude, frequency, duration, timing, and rate of change (Hughes and James, 1989; Poff and Ward, 1989; Richards, 1989; Poff, 1996; Richter and others, 1996, 1997, 1998; Clausen and Biggs, 1997, 2000; Puckridge and others, 1998; Clausen and others, 2000; Wood and others, 2000). The final database of hydrologic metrics in this study contains more than 90 traditional and ecologically relevant hydrologic metrics for each streamgage used in the analysis.

Streamflow and fish community data compiled for this analysis were not collected for the specific purposes of this study and largely resulted from data collection networks not designed to optimize collection of multiple types of data at a single site. Additionally, streamflow and fish community data

Table 1. Data-collection sites with fish-community sampling information and streamflow information.

[IBI, index of biotic integrity; rows with gray shading indicate sites used in primary analysis; BR, Blue Ridge; RV, Ridge and Valley; SA, Southwest Appalachians; IP, Interior Plateau]

Site (ecoregion) (streamflow data time period)	Drainage area (mi^2)	IBI rank (specialized insectivore value)	Land use (percentage)[a]		
			Forest	Agriculture	Developed
Davidson River (BR) (1988 – 2001)	15	good (0.665)	95.8	2.0	1.9
Ivy Creek (BR) (1987 – 2000)	158	good/excellent (0.544)	75.7	18.4	5.8
French Broad River (BR) (1988 – 2001)	1,858	good (0.789)	83.4	10.1	6.0
Pigeon River (BR) (1989 – 2002)	39	poor (0.034)	84.6	8.6	6.5
Pigeon River at Newport (BR) (1997 – 2000)	662	fair/good (0.652)	88.4	7.3	4.0
Nolichucky River (BR) (1991 – 2004)	805	excellent (0.678)	90.7	7.1	1.8
Big Limestone Creek (BR) (1997 – 2001)	79	fair/good (0.367)	17.4	75.6	6.8
East Fork Little Pigeon River (BR) (1989 – 2000)	63.5	fair (0.348)	89.4	9.4	0.8
South Fork Holston River (BR) (1988 – 2001)	38	fair/good (0.571)	83.6	15.3	1.0
Watauga River (BR) (1990 – 2003)	14	good (0.728)	87.9	9.0	2.1
North Fork Holston River (RV) (1988 – 2001)	53	good (0.505)	75.0	24.0	0.8
Big Creek (RV) (1989 – 2002)	47.3	poor/fair (0.304)	65.1	33.7	1.1
Little River at Wildwood (BR) (1988 – 2001)	274.2	good/excellent (0.46)	85.2	13.9	0.7
Little River at Rockford (BR) (1987 – 2001)	302	good (0.622)	74.1	20.7	4.6
Little Tennessee River (BR) (1988 – 2001)	19	good/excellent (0.439)	91.1	7.7	0.9
Nantahala River (BR) (1991 – 2004)	7	poor (0)	99.7	0.2	0.1
Oconaluftee River (BR) (1987 – 2000)	27	good (0.84)	98.8	0.7	0.3
Tellico River (BR) (1988 – 2004)	118	good (0.568)	97.0	1.9	1.1
Valley River (BR) (1990 – 2003)	104	good (0.399)	87.1	6.6	6.0
Limestone Creek (IP) (1989 – 2002)	119	poor/fair (0.087)	17.1	69.4	11.2
Clinch River (RV) (1988 – 2001)	56	good (0.7)	70.2	27.3	2.2
Powell River (RV) (1987 – 2000)	685	good/excellent (0.618)	79.6	17.8	2.2
Clear Creek (SA) (1997 – 2001)	170	fair (0.256)	---	---	---
North Mouse Creek (RV) (1993 – 2002)	36	poor (0.012)	57.4	36.6	5.4
West Chickamauga Creek (RV) (1987 – 2001)	175	fair (0.326)	67.8	25.5	6.3
Hester Creek (IP) (1998 – 2004)	57	fair (0.206)	56.8	43.1	0.1
Elk River (SA) (1991 – 2004)	68	fair (0.379)	85.7	11.9	0.8
Paint Rock River (IP) (1988 – 2001)	320	fair (0.368)	83.3	14.5	1.5
Shoal Creek (IP) (1990 – 2004)	330	good (0.428)	64.3	32.0	3.4
Wartrace Creek (IP) (1991 – 2004)	34.7	poor/fair (0.296)	49.2	48.4	0.9
Carters Creek (IP) (1991 – 2004)	32.5	good (0.426)	33.8	62.4	2.0
Piney River (IP) (1989 - 2002)	45.7	good (0.836)	76.4	23.6	0.0
Piney River (IP) (1989 – 2002)	190.6	fair/good (0.416)	73.8	23.7	2.2

[a] source: USGS (2001)

sites were located in both freeflowing and regulated streams downstream from large hydroelectric, flood control, or water supply reservoirs. For the purposes of this study, only free-flowing streams were considered because conclusions drawn from the analysis would most likely be applied to unregulated watersheds. The exclusion of regulated systems also increased the likelihood that the hydrologic characteristics identified might explain patterns in ecological data representative of relatively unaltered conditions.

Dataset compilation

Sites from the streamflow and fish community datasets were paired temporally and spatially using a geographic information system (GIS) to produce a composite dataset. Because the primary datasets were collected without reference to each other, some spatial extrapolation was needed to produce a statistically adequate number of paired sites. This is a difficulty common to researchers in the field of ecohydrology (Poff and Allan, 1995). In this study, a distance of three linear stream miles was chosen as the maximum distance that two paired sites could be separated. This choice was based on professional judgement that flow conditions along an approximately 5 km stream segment would be sufficiently uniform that hydrologic conditions at one point could be meaningfully related to fish community indices at another. Some site pairs were rejected because of tributary inflow between streamflow and fish community sample locations. Further, paired sites needed to have data collected in concurrent time periods. Fish community data commonly represent a single point in time, whereas the streamflow data represent a continuous time series. Concurrent collection of fish community data and streamflow data was required for site pairs used in this analysis to ensure that fish community data were reflective of the streamflow data used in the analysis.

The length of streamflow record was also limited to minimize the effects of any trends in streamflow such as those identified nationally in McCabe and Wolock (2002) and regionally in Wolfe and others (2003). In this study, no more than 15 years of streamflow data were used to avoid any long-term climatological trends while also providing sufficient data for calculation of hydrologic metrics. Hydrologic time periods were used up to 15 years prior to the time that the fish community sampling occurred, not including the year of the fish community sampling. A time series of up to 15 years of continuous streamflow data was used to calculate the hydrologic metrics at each site. The decision to omit streamflow data collected during the year of fish community sampling was based on the assumption that the current year hydrologic conditions had little to do with the adult year class of the fish population that is typically sampled, which is a product of previous years' hydrologic conditions.

Application of these temporal and spatial filtering techniques resulted in 33 sites (Figure 1c, Table 1) where streamflow and fish community data could be paired for analysis. Although the number of sites is small in regard to the available number of fish community sampling sites and streamgages in the Tennessee River Valley, the 33 sites used in the analysis represent locations where streamflow and fish community data can be analysed without concern over representativeness between data types. More liberal filtering of the two datasets could potentially introduce noise into the analysis such as increased intervening drainage area and point-source discharges.

BEST analysis

Multivariate correlation analysis using the spatially paired sites with concurrent hydrologic metrics (based on up to 15 years of streamflow data) and fish community data was performed using the dataset of 33 sites resulting from spatial and temporal filtering (Table 1). The analysis method used in this study is known as BEST and is an option in the Plymouth Routines in Multivariate Ecological Research (PRIMER) software (Clarke and Gorley, 2006). The procedure selects environmental variables that best explain community patterns by maximizing a rank correlation between the environmental (hydrologic metrics) and ecological (fish community) resemblance matrices. Fish IBI composite scores and component metrics were not used in this primary analysis so that any correlations with hydrologic metrics would be based on native species only and not on broader assemblage groupings (e.g. IBI metrics). The BEST procedure uses the Bray–Curtis similarity matrix of fish community data and conducts a stepwise search across the dataset containing the standardized hydrologic metrics (Clarke and Ainsworth, 1993). The stepwise procedure adds and removes environmental variables—in this case, hydrologic metrics—until the correlation coefficient between the hydrologic and fish community matrices is maximized. This procedure has been used to test relations between environmental and biological datasets in the fields of marine biology (Clarke, 1993), as well as terrestrial ecology (Edgerly and Rooks, 2004). In essence, the procedure selects the hydrologic metrics that best explain the multivariate pattern observed in the fish community data.

Hydrologic metrics were analysed separately as groups of related variables—magnitude, frequency, duration, timing, and rate of change as presented in Richter and others (1996). Statistical significance of the selected hydrologicmetric sets was evaluated using a permutation test in which the hydrologic metrics are randomly selected with the test statistic indicating the degree that a variable set differs from a randomly selected variable set. The termination criterion for the metric selection procedure was set at >0.95, and the $\Delta\rho$ was set at 0.001. Results of the BEST analysis were deemed significant if the values of ρ were significant at $\alpha = 0.1$ using 1,000 permutations of each subset of hydrologic metrics.

Quantile regression analysis

We used quantile regression analysis to define thresholds of potential ranges of insectivore scores for given values of the hydrologic metric(s) (Cade and others, 1999; Cade and Noon, 2003; Konrad and others, 2008). As with the BEST analysis, quantile regression analysis was based on up to 15 years of continuous streamflow data for the hydrologic metrics and the fish community data from a single sample. Quantile regressions are often discussed in terms of ceiling or floor relations (Cade and others, 1999; Cade and Noon, 2003; Konrad and others, 2008). The term 'ceiling relation' describes a quantile regression line that defines an upper threshold such that dependent variable values could be expected to be equal to or less than for tau (τ) percent of the time. Floor relations are inversely defined.

The hydrologic metrics identified through the analysis using fish community data were subsequently evaluated using the specialized insectivore score at each site. The specialized insectivore score, a component of the composite IBI score, was chosen for two reasons. First, insectivorous fishes, such as *Percinidae* darters, *Cyprinidae* minnows, and *Noturus* madtoms, are among the most jeopardized fish in the Tennessee River Valley (Etnier, 1997). Second, insectivorous fish represent a middle ground in the trophic structure of a stream, feeding on invertebrates while being prey for predator species. Subsequent analysis using invertebrate community data could complement this analysis and provide verification of the results presented here. The specialized insectivorous fish score is calculated by dividing the number of fish considered to be in the specialized insectivore trophic group by the total number of fish collected from in all trophic groups at the site.

Results and Discussion

BEST analysis

Results from the BEST analysis indicated a set of 16 hydrologic metrics that were significantly correlated with the multivariate assemblage patterns in the fish community (Table 2). These hydrologic metrics represent a broad spectrum of potentially ecologically relevant hydrologic metrics from the five flow categories (magnitude, frequency, duration, timing, and rate of change) in addition to low-, average-, and high-flow portions of the flow regime (discharge time series or hydrograph). Traditional hydrologic metrics such as low-flow values (7Q10), frequency of flood events (50-year flood), and flow-duration values were not identified as significant by this analysis.

Quantile regression

Three of the 16 hydrologic metrics identified through the analysis appear to be useful in response curve applications when comparing the insectivorous fish score to hydrologic metrics: streamflow constancy, frequency of moderate flooding, and rate of streamflow recession (Tables 2 and 3). Constancy, frequency of moderate flooding, and rate of streamflow recession each reveal a pattern of change between the metric value and an associated response in the specialized insectivore IBI metric. These three metrics have distinct response curves between the hydrologic metric and the IBI specialized insectivore component metric for which a functional connection can be proposed.

Constancy

Constancy is a measure of flow stability—the consistency of streamflow from one day to the next (Colwell, 1974; Poff, 1996). Constancy reflects average conditions and is most closely associated with base flows. Persistence of streamflow at base flow levels determines the available wetted perimeter of the channel. Stability of wetted perimeter corresponds to stable and available habitat for invertebrate colonization and subsequent uptake by insectivorous fish. Equally important, stability of base flow is critical to maintaining water quality conditions such as dissolved oxygen, temperature, and basic water chemistry (King and others, 2003; Postel and Richter, 2003).

Constancy has been documented as significant to increased densities of invertebrates in several studies. Poff and Ward (1989) identified constancy as a hydrologic descriptor distinguishing perennially flashy (low constancy) streams from more stable, groundwater dominated (high constancy) streams. Matthews (1988) associated increased constancy with opportunities for predation and competition sufficient to change community structure. Puckridge and others (2000) found that, in central Australia, higher values of constancy allow for colonization of new habitat areas and provide opportunities for fry to escape to areas with more agreeable hydraulic characteristics. Clausen and Biggs (1997, 2000) and Clausen and others (2000) found that values of constancy correlated positively with the density and richness of invertebrates and periphyton in studies of New Zealand streams. Increased density and richness of invertebrates and periphyton provide additional sources of food for insectivore fishes.

Table 2. Multivariate sensitivity analysis for relations between fish-community structure and hydrologic metrics (BEST model).

[Hydrologic metrics calculated without the data for the year the fish sampling occurred; model variables presented are significant at $\alpha \leq 0.1$; bolded values are significant at $\alpha \leq 0.05$; BEST output variables are defined in Table 3]

BEST Output (rho values and significant hydrologic variables)				
Magnitude	**Frequency**	**Duration**	**Timing**	**Rate**
0.32	0.38	0.29	0.39	0.25
MA26, MA41, ML18, ML20, MH10	FL2, FH6	DL6, DH13, DH16	TA1, TL1, TH1	RA5, RA7, RA8

Table 3. Hydrologic metric definitions with similar patterns to fish-community data resulting from BEST routine.

[nomenclature from Olden and Poff (2003); definitions from Henriksen *et al.* (2006) and Olden and Poff (2003)].

	Hydrologic parameter name	Definition (units)	Literature references [a]
Magnitude	MA26 – Variability of March streamflow	Compute the standard deviation for March streamflow and divide by the mean streamflow for March. (percent)	1, 3, 4, 5
	MA41 – Mean annual runoff	Compute the annual mean daily streamflow and divide by the drainage area. (cubic feet per second (cfs) per square mile)	9
	ML20 – Base flow	Divide the daily flow record into 5-day blocks. Assign the minimum flow for the block as a base flow for that block if 90 percent of that minimum flow is less than the minimum flows for the blocks on either side. Otherwise, set it to zero. Fill in the zero values using linear interpolation. Compute the total flow for the entire record and the total base flow for the entire record. ML20 is the ratio of total flow to total base flow. (dimensionless)	1, 2, 6
	MH10 – Maximum October streamflow	Maximum October streamflow across the period of record. (cfs)	10
	ML18 – Variability in base flow	Standard deviation of the ratios of 7-day moving average flows to mean annual flows for each year multiplied by 100. (percent)	5
Frequency	FL2 – Variability in low-pulse count	Coefficient of variation for the number of annual occurrences of daily flows less than the 25th percentile. (dimensionless)	3, 4, 5
	FH6 – Frequency of moderate flooding (three times median annual flow)	Average number of high-flow events per year that are equal to or greater than three times the median annual flow for the period of record. (number per year)	1, 2, 6
Duration	DH13 – Average 30-day maximum	Average over the period of record of the annual maximum of 30-day moving average flows divided by the median for the entire record. (dimensionless)	1
	DL6 – Variability of annual minimum daily average streamflow	Compute the standard deviation for the minimum daily average streamflow. Multiply by 100 and divide by the mean streamflow for the period. (percent)	3, 4, 5
	DH16 – Variability in high-pulse duration	Compute the standard deviation for the yearly average high-flow pulse durations (daily flow greater than the 75th percentile). (percent)	3, 4, 5
Timing	TA1 – Constancy	Measures the stability of flow regimes by dividing daily flows into predetermined flow classes. (dimensionless)	1, 2, 6, 7, 8
	TL1 – Annual minimum flow	Julian date of annual minimum flow occurrence. (Julian day)	1, 3, 4, 5
	TH1 – Annual maximum flow	Julian date of annual maximum flow occurrence. (Julian day)	1, 3, 4, 5
Rate of Change	RA5 – Number of day rises	Compute the number of days in which the flow is greater than the previous day divided by the total number of days in the flow record. (dimensionless)	1
	RA7 – Rate of streamflow recession	Compute the logarithm of flows and then compute the median change in log of flow for days in which the change is negative across the entire flow record. (flow units per day)	1
	RA8 – Flow direction reversals	Average number of days per year when flow changes from rising to falling (or from falling to rising). (number per year)	5

[a] (1) Clausen *et al.*, 2000; (2) Clausen and Biggs, 1997; (3) Richter *et al.*, 1996; (4) Richter *et al.*, 1997; (5) Richter *et al.*, 1998; (6) Clausen and Biggs, 2000; (7) Poff and Ward, 1989; (8) Poff, 1996; (9) Hughes and James, 1989; (10) Wood *et al.*, 2000

Quantile regression indicates a positive, ceiling relation between constancy and insectivore scores with the lower 80% of insectivore scores ($\tau = 0.80$, $P < 0.005$ that the coefficient is zero) (Figure 2a). Using the 80th percentile line in Figure 2a, the predicted value of the insectivore score for a given value of constancy would be equal to or less than the line value 80% of the time. Conversely, a predicted value of insectivore score would be greater than the line for a given value of constancy 20% of the time. There is an 80% probability that insectivore scores will vary from 0 to 0.70 for a constancy value of 0.60. Likewise, there is an 80% probability that insectivore scores will vary from 0 to 0.4 for a constancy value of 0.20. Increasing values of constancy at a site do not ensure higher insectivore score values; however, insectivore score potential is increasingly limited at sites with lower values of constancy.

Frequency of moderate flooding

The frequency of moderate flooding is defined as the average number of occurrences per year of floods with magnitudes that are at least 3 times the median annual flow. Several authors have speculated that the velocity and stream power associated with floods of this magnitude are sufficient to remove silt from the substrate (Clausen and others, 2000; Clausen and Biggs, 1997, 2000) and moderately disturb the bed material (Sagar, 1986; Grimm and Fisher, 1989; Death and Winterbourn, 1995). Decreased siltation and increased water clarity from decreased silt have proven to be beneficial to salmon (Greig and others, 2005) and sight-feeding fish (Zamour and Grossman, 2007). In our study, average stream velocities for the streamflow 3 times the median annual are 1.19, 0.49 and 0.20 m/s for the Oconoluftee River, North Fork Holston River, and Wartrace Creek (sites a, b, and c, respectively on Figure 3, 1988 water year used as a typical example; based on streamflow measurements retrieved from *http://nwis.waterdata.usgs.gov/*). These velocities appear sufficient to mobilize unconsolidated silt from the substrate and also are on the lower end of velocity needed to entrain the bed material relative to each site's substrate—gravel/cobble, gravel, and gravel/sand, respectively (Vanoni, 1977, Table II.46). However, higher streamflow velocities (higher magnitude floods) also mobilize unconsolidated silt and stimulate the substrate. The frequency of the flood equal to or greater than 5 times the median annual streamflow shows a similar pattern with regard to insectivorous fish scores to that of a flood, which is 3 times the median annual streamflow in our study.

In the Tennessee River Valley, insectivorous fish scores increased with the decreasing frequency of moderate flooding, whether using the 3- or 5-times median annual streamflow events for comparison. The negative correlation seen in our study using two different magnitudes of flood events indicates that the removal of silt from substrate is not the primary functional connection between this hydrologic metric and the fish community. The negative correlation we observed indicates that the frequency of occurrence is more important to the structure of the fish community than the magnitude

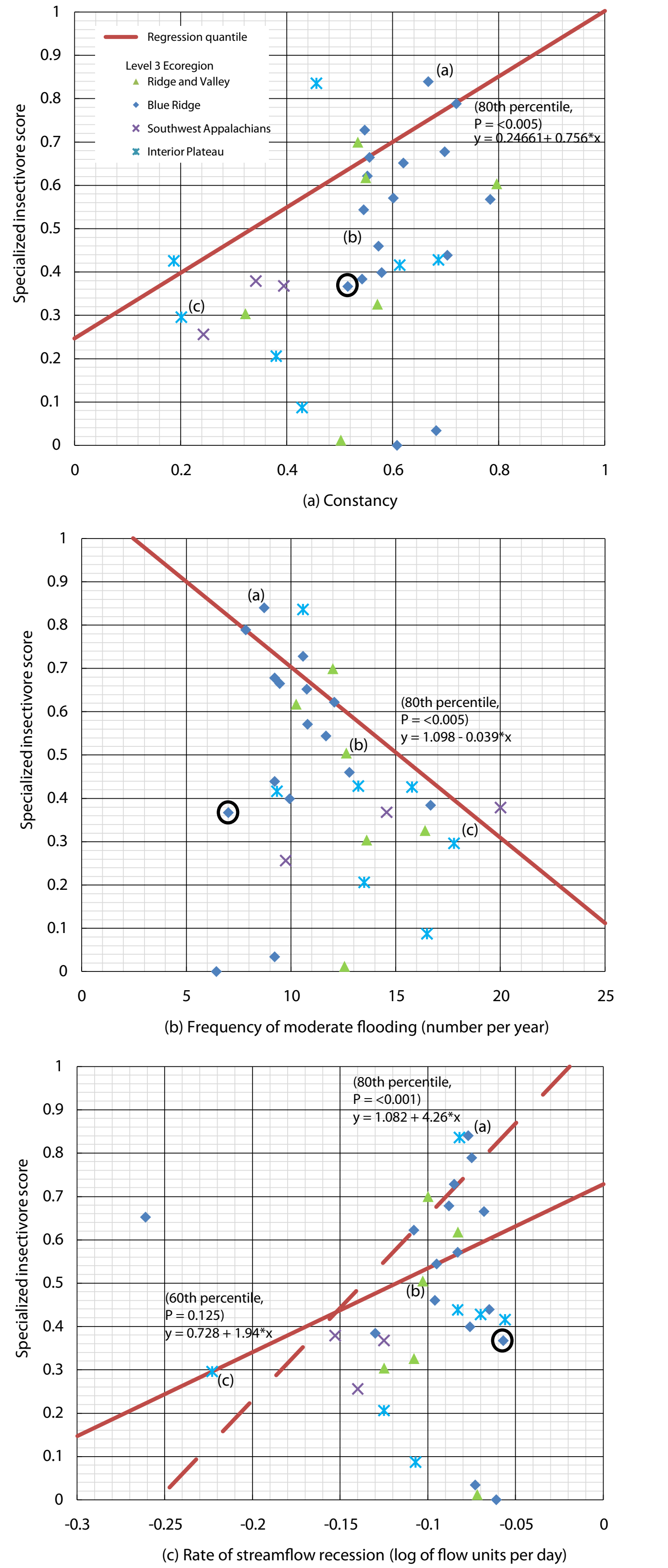


Figure 2. Comparison of three hydrologic metrics to the specialized insectivore component IBI scores with corresponding ecoregion Level 3 designation for sites in the Tennessee River Valley. [Letters in parentheses correspond to site hydrographs in Figure 3. Certain data points are circled or numbered because they are discussed in the text in detail.]

of the flood event—insectivorous fish respond positively to decreased disturbance. Habitat becomes increasingly unstable with increasing frequency of moderate floods, resulting in the decline of insectivorous fishes and invertebrates. This result mirrors findings from studies using invertebrates (Sagar, 1986; Death and Winterbourn, 1995), invertebrates and periphyton (Grimm and Fisher, 1989), and fish (Freeman and others, 2001). Sagar (1986) showed correlation between increased flood frequency and unstable streambed and an increase in invertebrate density with increasing time in stable streamflow. Findings by Death and Winterbourn (1995) and Grimm and Fisher (1989) also support this concept. Freeman and others (2001) show evidence of decreased young-of-year fish survival with increases of high-flow pulses. In contrast, the findings of Clausen and others (2000) and Clausen and Biggs (1997, 2000) show a positive, curvilinear relation between frequency of moderate flooding (increased disturbance) habitat siltation and invertebrates.

Quantile regression for the frequency of moderate flooding identifies a negatively correlated ceiling relation with the lower 80% of insectivore scores ($\tau = 0.8$, $P < 0.005$). Insectivore scores have the potential to increase when the frequency of moderate flooding decreases. Decreasing frequency of moderate flooding does not necessarily ensure higher insectivore scores, though higher frequency of moderate flood events limits insectivore scores.

Rate of streamflow recession

The rate of streamflow recession is a measure of how fast or slow streamflow recedes to baseflow following a flood peak. The rate of streamflow recession from runoff events can provide habitat-limiting factors for different segments of the fish community. High recession rates elicit several consequences in the stream, including stranding fish in isolated pools made available during high flows and limiting the amount of time for passage of fish between potential spawning and feeding areas—both consequences are types of hydrologic barriers. The idea of stranding or barricading is similar to the reduction in the viability of freshwater biota with decreased hydrologic connectivity concept presented in Freeman and others (2007). Freeman and others (2007) and Northcote and Hinch (2004) postulate that alteration of headwater stream connectivity to the larger river system by means of road crossings or culverts potentially inhibits spawning fishes from reaching optimal spawning grounds. Subsequently, fry are prevented from reaching suitable sites by unsuitable hydrologic and hydraulic conditions. Cushman (1985), Moog (2006), and Petts (1984) reiterated the concept of stranding or creating barriers to fish and invertebrate movement when recession rates are high, and they introduced the idea that quick recession increases invertebrate drift or movement, thereby depleting food sources.

Whiting (2002) noted that high-streamflow recession rates have been associated with saturated streambank failure, potentially increasing embeddedness through higher sediment loadings and decreasing the clarity of the water. Sediment deposition from bank failure also disrupts and diminishes available spawning and feeding habitat. Diminished habitat results in crowded conditions that result in hybridization between fish species, which is an undesirable occurrence. In conjunction with bank failure (decreased water clarity), rapidly changing hydraulic conditions (i.e. velocities) resulting from rapid streamflow recession rates would cause fish and invertebrates to become increasingly mobile to locate preferred habitat and food sources.

Quantile regression for the rate of streamflow recession indicates a positive, ceiling relation at the 60th percentile ($\tau = 0.60$, $P = 0.125$) (Figure 2c). The low quantile value for the RA7 (rate of streamflow recession) hydrologic metric is attributed to the outlier values of RA7 less than –0.20. If those site values are removed from the quantile regression, a similar positive ceiling relation exists with the lower 80% of insectivore scores ($\tau = 0.80$, $P < 0.001$) (Figure 2c, dashed line on RA7 plot). The potential range of values for specialized insectivore scores at a site decreases as the rate of streamflow recession increases (larger negative numbers). Multiple interactions among unmeasured environmental factors, such as water chemistry, are likely influencing the structure of the fish community causing low and high insectivore scores to occur at similar hydrologic-metric values for each hydrologic metric.

The rate of streamflow recession and constancy are functionally similar in that both measure the flashiness of streamflow; however, each metric represents a distinct characteristic of streamflow. Rate of streamflow recession (change in flow per day) considers only the segment of the hydrograph when streamflow decreases when compared to the previous day, or when streamflow decreases from one day to the next on the falling limb of the hydrograph. From the perspective of stream biota, this would be indicative of how quickly the habitat is being ‘drained’. Constancy (dimensionless) takes the entire hydrograph into consideration and measures how similar the streamflows are from one day to the next over the entire hydrograph. Within the stream, this would be similar to measuring the consistency of habitat inundation. The difference in these hydrologic metrics is that the streamflow recession rate represents a measure of streamflow *instability*, whereas constancy represents a measure of streamflow *stability*. Constancy increases when the rate of recession decreases, though the rate of recession is not the only factor represented by constancy. The example streams on Figure 3 show that as absolute values of streamflow recession rate increase, values of constancy decrease, meaning that flow stability of a stream decreases as the rate of recession increases. These two metrics are not entirely independent.

Physiographic analysis

Functionally, constancy, frequency of moderate flooding, and rate of streamflow recession vary according to the pathways used by water to travel from land surface to stream. These three hydrologic metrics represent characteristics of the streamflow hydrograph that are likely affected by landscape-scale processes. The explanation for the variability of hydrologic metrics and the response of insectivore scores presented in this study is physiohydrography. Land use data (Table 1) for the sites show that developed land use is generally less than 5% and that land use for watersheds draining to sites is predominately forest or agriculture (U.S. Geological Survey, 2001). Physiohydrographic factors directly affecting the streamflow hydrograph, and fish communities by association, include channel and basin gradient, soils (soil and regolith thickness, texture, permeability, etc.), habitat (substrate type), and base-flow (groundwater availability and discharge) (Vannote and others, 1980; Minshall and others, 1983; Resh and others, 1988). Areas with a similar physiohydrography are captured at a coarse level with the Level 3 ecoregion boundaries as defined by Omernik (1987).

The response curves for hydrologic metrics reflect spatial groupings based on Level 3 ecoregions (Figure 2, Table 4). The functional definitions of the hydrologic metrics coincide with the physiohydrographic characteristics of each ecoregion. Generally, Blue Ridge and Interior Plateau ecoregion sites occupy opposite ends of the response curves of Figure 2, though Interior Plateau sites in the Highland Rim have characteristics similar to Blue Ridge sites. With each hydrologic metric presented in this paper, watersheds in the Ridge and Valley represent a middle ground or blending of the physiohydrography of the two end members. Constancy, the stability of streamflow, is generally highest in Blue Ridge streams and lowest in streams of the Interior Plateau (Figure 2a). This difference reflects regional patterns of soil thickness and karst development. Additionally, Blue Ridge watersheds have a limited snow pack at the high elevations which results in protracted seasonal runoff as temperatures increase in the spring, though impact on the stream hydrograph in Blue Ridge streams is likely limited. The frequency of moderate floods is highest in the Interior Plateau and lowest in the Blue Ridge (Figure 2b). This is probably the result of decreased soil thickness, increased surficial bedrock, and well-developed karst terrain. Rainfall in the Interior Plateau, relative to the Blue Ridge, is not retained in storage and is routed to streams through karst conduits. The process of routing precipitation to streams through karst conduits can occur in a matter of hours in Nashville/Bluegrass Basins (Knight and Kingsbury, 2007). Williams and others (2006) provide evidence of longer transport times along the Highland Rim. Rate of streamflow recession is generally lowest in the Blue Ridge and highest in the Interior Plateau. This is the result of a combination of factors previously mentioned. Well-developed karst terrain in the Interior Plateau and Ridge and Valley provides an efficient method of delivering rainfall from the surface to a stream, and is not present in Blue Ridge streams at the same scale or spatial extent. Conversely, thick soils and a large percentage of forest cover slow the runoff to the stream, consequently providing a low streamflow recession rate. Streams in the Ridge and Valley are represented by moderate values for each of the hydrologic metrics as a result of the blending of physiohydrography represented in that ecoregion (Figure 2c).

Streamflow hydrographs from three sites— Oconoluftee River (Blue Ridge), North Fork Holston River (Ridge and Valley), and Wartrace Creek (Interior Plateau)—are provided as graphical examples of sites in the study area bridging the spectrum of hydrologicmetric values, IBI component scores, and ecoregions from sites in this study (Figure 3). The Oconoluftee River has a constancy value of 0.67 (Figure 3a), whereas the North Fork Holston River (Figure 3b) and Wartrace Creek (Figure 3c) have values of 0.50 and 0.20, respectively; insectivore scores for each of these sites range from 0.84 to 0.30. Values for the frequency of moderate flooding were 8.7, 12.6, and 17.8 for the Oconoluftee River, North Fork Holston River, and Wartrace Creek, respectively. In this study, the frequency of moderate flooding varied from approximately 6 to 20 events per year, whereas the insectivore scores varied from approximately 0.9 to 0.2. These three comparison sites have values for rate of streamflow recession of –0.08, –0.10, and –0.22 for the Oconoluftee River, North Fork Holston River, and Wartrace Creek, respectively. As values of the rate of streamflow recession increase negatively (large negative values represent greater streamflow change or steeper falling limb slopes), insectivore scores decrease.

Complicating factors

The interior distribution of point pairs below the quantile regression lines shown in Figure 2 indicates that variability in specialized insectivore scores cannot be explained by the hydrologic metrics alone. Multiple interactions with unmeasured environmental factors, such as water chemistry, influence the structure of the fish community, causing low insectivore scores to occur at some sites with otherwise favourable hydrologic-metric values. Water quality parameters, such as nutrient and sediment concentration and dissolved oxygen, affect fish communities. However, water quality information is often spatially limited and is difficult to evaluate consistently over large areas.

Big Limestone Creek, circled on the plot of frequency of moderate flooding in Figure 2, provides an example of how water quality and other factors can complicate the interaction between fish communities and streamflow. This site has a favourable value of 7 for frequency of moderate flooding. This value should allow a high insectivore score. The insectivore score at this site is 0.367, less than half the value for other Blue Ridge streams with this hydrologic-metric value. There are at least two factors related to water quality that may explain lower insectivore scores. One factor is the high background nutrient concentrations at this site (1.7 mg/l) of nitrite plus nitrate and 0.07 mg/l of total phosphorus) (Flohr and others, 2002). These values are high in comparison to regional guideline concentrations for reference streams of 1.22 mg/l of nitrite plus nitrate and 0.04 mg/l of total phosphorus (Arnwine and Sparks, 2003). This high nutrient concentration has likely contributed to a change in the fish community structure from

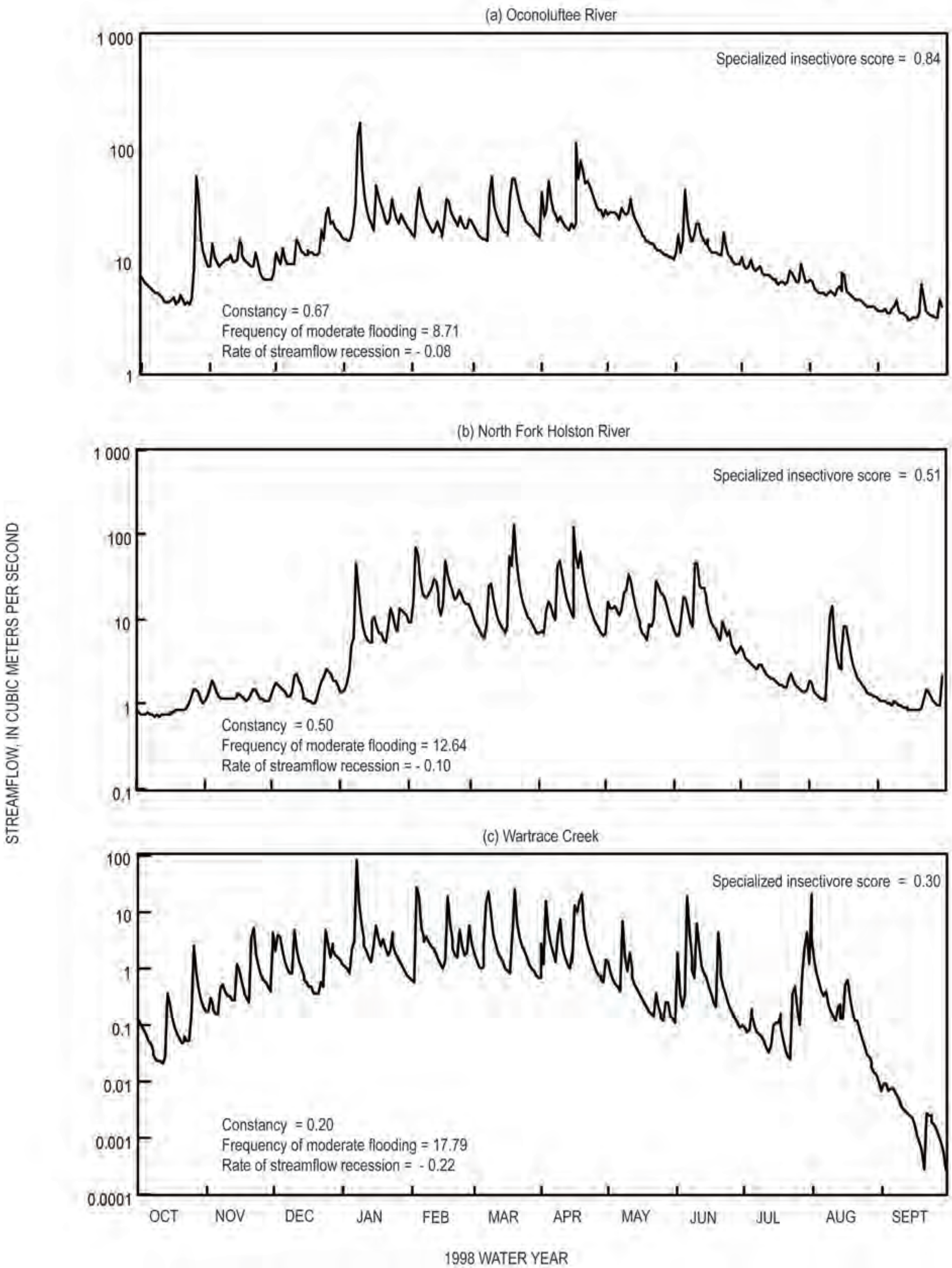


Figure 3. Streamflow hydrographs from three sample locations representing (a) Blue Ridge, (b) Ridge and Valley, and (c) Interior Plateau ecoregions and a range of three hydrologic metric values for the 1988 water year. [Letters in parentheses correspond to lettered points on graphs in Figure 2.]

Table 4. Low, median, and high values for constancy, frequency of moderate flooding, and rate of streamflow recession for 31 sites used for analysis organized by Level 3 Ecoregion.

Ecoregion	Constancy			Frequency of Moderate Flooding			Rate of Streamflow Recession		
	Low	Median	High	Low	Median	High	Low	Median	High
Blue Ridge	0.51	0.59	0.78	6.43	9.69	58	-0.26	-0.08	-0.06
Ridge and Valley	0.19	0.46	0.69	9.33	12.15	18	-0.22	-0.083	-0.06
Interior Plateau	0.32	0.52	0.80	10	12.60	58	-0.12	-0.10	-0.07
Southwest Appalachians	0.24	0.34	0.40	9.75	14.57	20	-0.15	-0.14	-0.12

insectivores to algivorous fishes. A second factor is repeated fish kills caused by episodic and acute ammonia concentrations (Hampson and others, 2000). High nutrient concentrations likely relate to the high percentage of agricultural land use in the basin (Table 1). In addition, karst geomorphology and hydrology of the basin may aggravate or ameliorate the delivery of high nutrient loads to the stream. What is clear is that water quality, episodic and acute events, and geochemistry can influence the health of fish communities. What remains to be understood is how these complicating factors interact with the hydrology of rivers to produce an ecological outcome.

Conclusion

Fish community structure is governed by numerous environmental factors, including streamflow characteristics, water chemistry, and human manipulation. Watershed management decisions that minimize change in these factors, or return any of them to predevelopment levels, have the potential to increase the health of the fish community. However, managing a single factor to restore it to predevelopment condition will not guarantee improvement in fish community health; it only allows for the potential response provided all other factors are restored. As optimal values for one environmental factor, such as streamflow, are achieved, other environmental factors are likely to limit the response of the fish community.

Constancy, frequency of moderate flooding events, and rate of streamflow recession are three hydrologic metrics with functional connections relevant to fish communities in streams located in the Tennessee River Valley. These hydrologic metrics explain a significant portion of the variation in the fish community structure on the basis of multivariate correlation analysis. These metrics appear to be limiting environmental factors on specialized insectivores at some sites. They are useful for estimating the potential specialized insectivore component of the fish community, but not necessarily the actual component score. A multidimensional approach that includes physiographic and water quality variables in the context of biogeographic potential is needed to identify other limiting environmental factors when comparing hydrologic metrics against specialized insectivore component scores.

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