RIVER RESEARCH AND APPLICATIONS

River Res. Applic. 27: 956-966 (2011)

Published online 21 May 2010 in Wiley Online Library (wileyonlinelibrary.com) DOI: 10.1002/rra.1400

USING HABITAT GUILDS TO DEVELOP HABITAT SUITABILITY CRITERIA FOR A WARMWATER STREAM FISH ASSEMBLAGE

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ABSTRACT

The diversity of fish species found in warmwater stream systems provides a perplexing challenge when selecting species for assessment of instream flow needs from physical habitat analyses. In this paper we examined the feasibility of developing habitat suitability criteria (HSC) for the entire fish community of a warmwater stream using habitat guilds. Each species was placed *a priori* into a guild structure and habitat data were collected for depth, velocity, Froude number, distance to cover, embeddedness and dominant and subdominant substrate. Correct guild classification was tested with linear discriminant analysis for each species. Correct classification based on habitat-use data was highest for riffle and pool-cover guilds, whereas the fast-generalist and pool-run classes, the broader niche guilds, were more frequently misclassified. Variables most important for discriminating guilds were Froude number, velocity and depth in that order. Nonparametric tolerance limits were used to develop guild suitability criteria for continuous variables and the Strauss linear index was used for categorical variables. We recommend the use of a wide array of variables to establish more accurate habitat analysis. Additionally, guild HSC can be developed with similar effort to that needed to develop HSC for a small number of individual species. Results indicate that a habitat guild structure can be successfully transferred to another river basin and that habitats for a diverse fish assemblage can be adequately described by a small number of habitat guilds. This approach represents an alternative for incorporating entire fish assemblages into habitat analyses of warmwater stream systems. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: habitat guilds; habitat suitability criteria; instream flow; physical habitat analyses; warmwater streams; fish assemblages

Received 11 May 2009; Revised 16 September 2009; Accepted 4 March 2010

INTRODUCTION

Advances in modelling hydrodynamics of natural stream channels, including two- and three-dimensional models, provide more spatial resolution in habitat conditions. Yet these tools need to be integrated with habitat-use descriptors for resident flora and fauna so flow-habitat tradeoffs can be accurately described. Instream Flow Incremental Methodology (IFIM), Physical Habitat Simulation (PHABSIM), MesoHABSIM (Parasiewicz, 2001), EVHA (Ginot, 1995) and similar systems are valuable tools for resource agencies to use when facing the difficult challenge of managing stream resources. The effectiveness of these techniques depends on the accuracy of the data used to describe the habitat needs of aquatic communities (Orth, 1995; Freeman *et al.*, 1997; Mouton *et al.*, 2007). A species' habitat is described by stream-specific or previously established

habitat suitability criteria (Bovee, 1986; Crance, 1987). If the habitat datum used is inaccurate then modelling efforts will fail to determine how changes in stream flow affect the habitat available to a species or group of species (Waite and Barnhart, 1992; Bovee, 1994).

While accurate habitat data is necessary for habitat analysis, the data also needs to represent the entire aquatic community (Moyle and Baltz, 1985; Orth, 1987; Gan and McMahon, 1990). Having habitat information for only one or two species in warmwater stream systems limits the usefulness of habitat model output. If only a small portion of the community is represented, then flows thought to protect the integrity of the system may actually be detrimental to it (Bain *et al.*, 1988; Lobb and Orth, 1991; Aadland, 1993). Using habitat guilds to represent the habitat needs of the aquatic community has been proposed as a solution to this problem (Orth, 1987; Leonard and Orth, 1988; Lobb and Orth, 1991; Aadland, 1993; Welcomme *et al.*, 2006).

Habitat guilds are treated as super species and their criteria are established from the data collected for all members of the guild (Gorman, 1988; Austen *et al.*, 1994). This way all members of the guild are represented by the guild criteria. The drawback of this approach is the lack of

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accurate habitat information for many species, which makes guild placement difficult (Angermeier, 1987). The difficulty of guild placement is an important consideration because species placed incorrectly will create inaccurate habitat criteria. Therefore, the placing of species into the proper guild is a principal task in developing habitat criteria.

Several different guild structures have been proposed for use in instream flow studies with the number of guilds being used varying from 4–7 (Bain *et al.*, 1988; Lobb and Orth, 1991; Aadland, 1993; Vadas and Orth, 1997; Vadas and Orth, 2000). The habitat guild structures proposed have always been developed in the system being studied. The establishment of site-specific guilds requires a large amount of data to be gathered on the fish community. This is at odds with the main purpose of using the guild approach, which is to reduce the data needed to establish habitat criteria. Guild structures need to be able to transfer to similar systems with little or no alterations if this approach is to be useful.

Fish habitat research has progressed little in determining the best way to use guilds in developing habitat suitability criteria (with the exception of Vadas and Orth, 2001) or if guild structures established in one system can be used elsewhere. In this study we evaluate the validity of using a habitat guild approach and examine alternative ways to establish habitat criteria for a warmwater stream fish community.

METHODS

Site description

This study focused on the North Fork Shenandoah River basin located in the Ridge and Valley Physiographic Province of northwestern Virginia. Our sampling sites ranged from 30 to 130 km upstream of the river's confluence with the South Fork Shenandoah River. The study sites for the summer of 2001 and 2002 were selected based on a mesohabitat assessment of the North Fork Shenandoah River, conducted during the fall of 1998 and spring of 1999 by Don Hayes and Peter Ruhl of the United States Geologic Survey (Krstolic et al., 2006). Seven fish sampling locations for the North Fork Shenandoah River were selected to proportionally represent the predominant habitat types (riffle, run, pocket run and pool) found throughout the river. Flow levels during summer sampling (June-September) were at historic lows, ranging from 3.5 to $228.5 \text{ m}^3 \text{ s}^{-1}$ in 2001 and 2.0 to $22.8 \text{ m}^3 \text{ s}^{-1}$ in 2002, at the Strasburg gagging station (USGS #01634000).

Habitat sampling

We conducted fish and habitat sampling using direct underwater observation and electrofishing using a throwable anode. The use of two separate sampling techniques allowed for a wide range of habitats and species to be sampled at a higher efficiency than either technique would have individually (Persinger *et al.*, 2004). Snorkelling surveys were conducted using modified static-drop techniques described by Li (1988). After lanes were established, the snorkelers moved slowly upstream along the ropes and dropped a marker at each fish location. All fish were identified to species except for the satinfin shiner (*Cyprinella analostana*) and the spotfin shiner (*Cyprinella spiloptera*). These two species were identified to genus because of the difficulty involved in field identification and will be referred herein as *Cyprinella* spp.

We used a stratified random sampling method to quantify the range of available habitat in the North Fork Shenandoah River (Grossman and Skyfield, 2009). Prior to sampling, an initial distance within 6 m of the starting point of the sample was chosen at random; a marker was placed at this point during the survey and at 6 m intervals through the rest of the sampling area. After the survey was completed, we returned to each marked location and measured the habitat. The dominant substrate, subdominant substrate, embeddedness and cover were described within a 1 m² area around all marked fish and random locations using a modified version of the Wentworth classification system (Bovee, 1982). Water column depth (m), mean water column velocity (m s⁻¹) and distance to nearest cover (m) were also measured.

For electrofishing using a throwable anode the river was divided into five equal sized lanes and sampled using a modified version of the diamond-sampling pattern (Bovee, 1994). Even if no fish were captured, all sampled locations were marked to get available habitat data. Collected fish were identified to species and recorded. The group would then proceed to the next sampling site. After the run was completed, the same habitat variables recorded during the snorkelling surveys were measured at all marked locations. For a complete description of the fish sampling techniques see Persinger *et al.* (2004).

Froude number was calculated for all the data points using the measured site depth and velocity:

$$F = v/(gd)^{1/2}$$

where v is equal to the mean water column velocity, d is equal to water column depth and g is equal to gravity (Gordon *et al.*, 1992).

Guild structure selection and testing

The habitat guild structure used in this study is a modified version of one developed for the Roanoke River, VA (Vadas and Orth, 1997, 2000). The guilds used in this study are riffle, fast generalist, pool-run and pool-cover (Figure 1). The riffle, fast generalist and pool-cover





Figure 1. Diagrams of the guild structures used for this study. The Vadas and Orth (2000) structure served as the basis for the creation and implementation of the North Fork Shenandoah guild structure

guilds are each a combination of two guilds described by Vadas and Orth (2000). The pool-run guild was unchanged from Vadas and Orth (2000). Guilds were combined due to the similarity of the habitat described by the guilds, a lack of habitat that matched a guild or a lack of species that fit into a guild.

Prior to sampling, the adult life stages of all species were classified into the four habitat guilds based on Vadas and Orth (2000) or on habitat information taken from literature. Due to a lack of literature information on the habitat use of the juvenile and age-0 life stages, these life stages were not placed initially. The species placement and guild structure were tested using collected habitat measurements.

Discriminant analysis was used to examine the existence of the guilds in the North Fork Shenandoah River, the species placement in the habitat guilds, and to develop a linear discriminant function for placing the other life stages. The existence of the guilds was tested using the Mahalanobis squared distance between the guilds at a significance level of 0.05 and using a misclassification matrix. Species placement was examined using the linear discriminant function to calculate guild placement for every data point of each species. SAS version 8e (SAS, 2000) was used for all statistical analysis.

Guild habitat suitability criteria

The data collected for all species assigned to a given guild were combined to form the data set used to develop the habitat suitability criteria. Criteria for each guild were developed for depth, velocity, Froude number, substrate, embeddedness, cover presence and distance to cover. Nonparametric tolerance limits were used to create criteria for the continuous variables depth, velocity, Froude number and distance to cover (Newcomb et al., 2007). Strauss Linear Index was used to create habitat suitability criteria for the categorical variables substrate, embeddedness, cover presence, and distance to cover (Strauss, 1979). The substrate criteria included the dominant substrate and subdominant substrate. Cover presence was based on whether or not cover could be found within a 1 m area of the fish location. Distance to cover criteria was developed using both nonparametric tolerance limits and Strauss Linear Index because the data was collected as continuous data out to a distance of 0.5 m, but all measurements greater than 0.5 m were grouped into a single category (>0.5 m). Criteria developed using both techniques were compared to determine if it should be treated as a categorical or continuous variable.

The nonparametric tolerance limits were used to construct type-III habitat suitability criteria for all species. The tolerance limits for the central 50% were used to establish the cutoffs for optimal habitat, which had a suitability value of one. The data located between the central 50% tolerance limits and the central 75% were given a suitability value of 0.5. The data located between the central 75% tolerance limits and the central 90% received a suitability value of 0.2. The data beyond the central 90% tolerance limit received a suitability of zero and were considered unsuitable habitat.

The Strauss Linear Index (L) was used to develop habitat suitability criteria for the categorical variables. The linear index is the statistical difference in the proportion of species use versus the proportion of availability. The sampling variance of the linear index allows a statistical comparison between the calculated value and the Null-hypothesis value of zero (Strauss, 1979). The linear index was calculated at an alpha of 0.05 for each level of the five categorical variables. Criteria were developed for each variable using the index values and the significance tests. Values with positive significance were considered optimal habitat and given a suitability of one. Negatively significant values were considered unsuitable habitat and given a suitability level of zero. Non-significant categories were considered usable habitat and given suitability values of 0.5 for positive values and 0.2 for negative values.

Table I. *p*-values for a test of the Mahalanobis squared distance between the guilds. Null hypothesis being tested is no significant difference between the guilds. A 0.05 *p*-value was used to determine significance

	Riffle	Fast Generalist	Pool/ Run	Pool- cover
Riffle	1.0000			
Fast Generalist	< 0.0001	1.0000		
Pool/Run	< 0.0001	< 0.0001	1.0000	
Pool-cover	< 0.0001	< 0.0001	< 0.0001	1.0000

Table II. Linear discriminant function for habitat guilds

Variable	Riffle	Fast Generalist	Pool/ Run	Pool- cover	
Constant	-26.836	-26.493	-28.346	-28.893	
Depth	9.865	11.860	13.832	14.692	
Velocity	-13.661	-12.556	-16.009	-18.056	
Distance to Cover	5.220	7.909	7.867	8.358	
Dominant substrate	2.400	2.345	2.376	2.421	
Subdominant substrate	1.891	1.900	1.932	1.866	
Embeddedness	7.404	7.272	7.726	8.050	
Froude number	41.662	36.072	41.607	42.212	

RESULTS

Guild structure testing

The data collected for the adult life stages of all species that were placed *a priori* into the guild structure were used to run a discriminant analysis of the guild structure. The Wilks Lambda statistic had a *p*-value of <0.0001 indicating that there were significant differences among the groups. Mahalanobis distance test (Table I) found each guild was significantly different from the other three guilds. The linear discriminant function was used to determine what habitat variables were most important to each guild; Froude number, velocity and depth, respectively, were the three most important variables for all four guilds (Table II). Embeddedness was the fourth most important variable for the riffle guild while distance to cover was the fourth most important for the other three guilds.

A misclassification matrix of all the data points (Table III) had an overall accuracy of 46.7%. For two guilds (riffle 64.4% and pool-cover 58.9%) the majority of data points were assigned to the correct guild. For the fast generalist guild, the highest percentage (42.7) of data points was assigned to the proper guild, but a large percentage (32.6) of data points were assigned to the riffle guild. The pool-run guild had only 8.9 per cent of the data assigned to the proper guild.

The linear discriminant function was used to confirm the a priori placement of species into the guilds and place the juvenile and age-0 life stage groups that were significantly different in their habitat use from the adult life stages into guilds by calculating the proper guild for each data point. Several a priori placed species had a higher percentage of their data in a guild different from the one in which they were assigned. The two main reasons for this were a lack of observations for a species (e.g. tessellated darter, Etheostoma olmstedi) or a lack of good habitat information on which to base guild placement for a species (e.g. river chub, Nocomis micropogon); however, no species was moved to another guild because the guilds themselves were significantly different from each other. Each juvenile and age-0 life stage was placed into the guild with the highest percentage of its data points (Table IV).

Guild habitat suitability criteria

The riffle and fast generalist guild's habitat suitability criteria indicate they are using a smaller range of depth and shallower depths than the pool-run and pool-cover guilds (Figure 2). The velocity criteria (Figure 3) indicate that the riffle guild is using the widest range and fastest velocities, pool-run and fast generalist guilds are using the intermediate velocities, and pool-cover guild is using the slowest velocities. The criteria developed for Froude number (Figure 4) shows a virtually identical pattern to that seen in the velocity criteria.

Table III. Number of guild species observations and per cent classified into each guild. The total column is the overall number of observations for the guild species. Overall accuracy = 46.7%

Actual Guild Membership		Number and Per cent of Guild Species Observed As:					
	Riffle	Fast Generalist	Pool/Run	Pool-cover	Total		
Riffle	217 (64.4)	90 (26.7)	11 (3.3)	19 (5.6)	337 (100)		
Fast Generalist	120 (32.6)	157 (42.7)	22 (6.0)	69 (18.8)	368 (100)		
Pool/Run	59 (25.1)	82 (34.9)	21 (8.9)	73 (31.1)	235 (100)		
Pool-cover	47 (12.8)	83 (22.6)	21 (5.7)	216 (58.9)	367 (100)		

Table IV. Final guild placement of the North Fork Shenandoah River species

Species	Guild	Ν	R	FG	PR	PC
Greenside darter (<i>Etheostoma blenniodies</i>)	R	1	1.00	0.00	0.00	0.00
Mottled sculpin (Cottus bairdi)	R	237	0.57	0.33	0.04	0.06
Central stoneroller (Campostoma anomalum)	R	29	0.76	0.17	0.03	0.03
Longnose dace (Rhinichthys cataractae)	R	70	0.81	0.14	0.01	0.03
Bluehead chub (Nocomis leptocephalus) (J)	R	23	0.52	0.35	0.04	0.09
River chub (Nocomis micropogon) (Y)	R	9	0.44	0.11	0.11	0.33
Potomac sculpin (Cottus girardi)	FG	1	0.00	1.00	0.00	0.00
Margined madtom (Noturus insignis)	FG	81	0.27	0.47	0.07	0.19
Rosyface shiner (Notropis rubellus)	FG	16	0.63	0.31	0.00	0.06
Comely shiner (Notropis amoenus)	FG	13	0.23	0.54	0.08	0.15
Spotfin/satinfin shiner (Cyprinella spp.) (A)	FG	211	0.29	0.42	0.06	0.23
Bull chub (<i>Nocomis raneyi</i>)	FG	1	0.00	0.00	0.00	1.00
Bluehead chub (Nocomis leptocephalus) (A)	FG	43	0.56	0.33	0.07	0.05
Blacknose dace (<i>Rhinichthys atrastulus</i>)	FG	2	1.00	0.00	0.00	0.00
Fallfish (Semotilus corporalis) (J&Y)	FG	44	0.20	0.52	0.05	0.23
Tessellated darter (<i>Etheostoma olmstedi</i>)	PR	1	0.00	1.00	0.00	0.00
Common shiner (Luxilus cornutus)	PR	23	0.43	0.57	0.00	0.00
River chub (Nocomis micropogon) (A&J)	PR	69	0.42	0.41	0.06	0.12
Fallfish (Semotilus corporalis) (A)	PR	51	0.18	0.51	0.12	0.20
Rosyside dace (Clinostomus funduloides)	PR	1	0.00	0.00	0.00	1.00
Green sunfish (Lepomis cyanellus) (A&J)	PR	45	0.09	0.11	0.13	0.67
White sucker (<i>Catostomus commersoni</i>)	PR	6	0.00	0.00	0.00	1.00
Northern hog sucker (<i>Hypentelium nigricans</i>)	PR	39	0.18	0.23	0.10	0.49
Banded killifish (Fundulus diaphanus)	PC	1	0.00	0.00	0.00	1.00
Swallowtail shiner (Notropis procne)	PC	1	0.00	1.00	0.00	0.00
Spottail shiner (Notropis hudsonius)	PC	14	0.14	0.36	0.07	0.43
Bluntnose minnow (<i>Pimephales notatus</i>)	PC	54	0.26	0.31	0.06	0.38
Common carp (Cyprinus carpio)	PC	1	0.00	0.00	0.00	1.00
Pumpkinseed (Lepomis gibbosus)	PC	1	0.00	0.00	0.00	1.00
Bluegill (Lepomis macrochirus)	PC	1	0.00	0.00	0.00	1.00
Redbreast sunfish (Lepomis auritus)	PC	206	0.06	0.15	0.04	0.75
Largemouth bass (<i>Micropterus salmoides</i>)	PC	7	0.00	0.00	0.00	1.00
Smallmouth bass (Micropterus dolomieu)	PC	138	0.17	0.29	0.04	0.50
Rock bass (Ambloplites rupestris)	PC	71	0.14	0.27	0.07	0.52
Brown bullhead (Ameiurus nebulosus)	PC	4	0.00	0.25	0.00	0.75
Yellow bullhead (Ameiurus natalis)	PC	35	0.08	0.29	0.06	0.57
Channel catfish (<i>Ictalurus punctatus</i>)	PC	1	0.00	0.00	0.00	1.00
Spotfin/satinfin shiner (<i>Cvprinella</i> spp.) (J&Y)	PC	46	0.13	0.28	0.04	0.54
Bluehead chub (<i>Nocomis leptocephalus</i>) (Y)	PC	11	0.18	0.27	0.00	0.55
Green sunfish (Lepomis cyanellus) (Y)	PC	27	0.11	0.26	0.00	0.63

R, riffle; FG, fast generalist; PR, pool-run; and PC, pool-cover. *N* is the number of observations for each species or life stage collected. Species that showed differences in habitat use based on life stage were assigned to guilds separately for each life stage. The letter in parenthesis following the name represents the life stage. A, adult; J, juvenile; Y, young of year and no letter means all life stages grouped together. The decimal fraction of data assigned to a guild is listed in the guild-specific columns. The percentage of data assigned to a guild is listed in the guild-specific columns.

Optimal substrate habitat for riffle guild and fast generalist guild ranges from small cobble to small boulder. Suitable habitat ranges from large gravel to flat bedrock for the riffle guild and from small gravel to flat bedrock for the fast generalist guild (Figure 5). Pool-run guild optimal substrate ranges from large cobble to small boulder with suitable habitat ranging from small cobble to tilted bedrock (Figure 6). Small cobble is the optimal habitat for the poolcover guild and all other substrate types except tilted bedrock is considered suitable (Figure 6).

The riffle, fast generalist and pool-run guilds all have the same criteria for embeddedness with 0-25% embeddedness being optimal habitat and anything more embedded considered unsuitable (Figure 7). The pool-cover guild has an optimal embeddedness of 25–50%, with anything greater than 25% being suitable (Figure 7).

The cover presence criteria indicated that all four guilds preferred locations with cover (Figure 8). The distance to cover HSC was created using both nonparametric tolerance limits and Strauss linear index values. For the



Figure 2. Depth habitat suitability criteria created using nonparametric tolerance limits for the four guilds sampled in the North Fork Shenandoah River during the summers of 2001 and 2002. Line width gradients are the central 50% (thickest line), central 75% (medium line), and the central 90% (thinnest line). For each guild the sample totals are: riffle n = 338, fast generalist n = 351, poolrun n = 194, and pool-cover n = 415

riffle guild and the fast generalist guild the Strauss criteria indicate that they need to be much closer to cover than is indicated with the tolerance limits (Figure 9). Although both sets of criteria cover similar ranges, the suitability of the Strauss criteria declines at a faster rate for the pool-run and pool-cover guilds than the tolerance limits criteria (Figure 9).



Figure 3. Velocity habitat suitability criteria created using nonparametric tolerance limits for the four guilds sampled in the North Fork Shenandoah River during the summers of 2001 and 2002. Line width gradients are the central 50% (thickest line), central 75% (medium line), and the central 90% (thinnest line). For each guild the sample totals are: riffle n = 338, fast generalist n = 351, pool-run n = 194, and pool-cover n = 415



Figure 4. Froude number habitat suitability criteria created using nonparametric tolerance limits for the four guilds sampled in the North Fork Shenandoah River during the summers of 2001 and 2002. Line width gradients are the central 50% (thickest line), central 75% (medium line), and the central 90% (thinnest line). For each guild the sample totals are: riffle n = 338, fast generalist n = 351, pool-run n = 194, and pool-cover n = 415



Figure 5. Riffle guild and fast generalist guild substrate habitat criteria. The guild bars represent the frequency that the substrate category was used by members of the guild and the available bars represent the frequency that substrate was found in all sampled locations in the North Fork Shenandoah River. The number of observations used were: riffle guild N = 676, fast generalist guild N = 702, and available N = 3176. Suitability values were based on the significance of the Strauss linear index values calculated

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1.0 0.5 Habitat Use Percent Frequency 0.8 0.4 vailable 0.6 0.3 Suitability 0.2 0.1 0.0 0.0 **Pool-Cover Guild** 0.5 1.0 Percent Frequency 0.8 0.4 Suitability 0.6 0.3 0.2 0.0 0.0 Copple Boulder bedrock cobble Boulder bedrock 3and Travel ravel Gravel Detritu

Substrate Type

Figure 6. Pool-run guild and pool-cover guild substrate habitat criteria. The guild bars represent the frequency that the substrate category was used by members of the guild and the available bars represent the frequency that substrate was found in all sampled locations in the North Fork Shenandoah River. The number of observations used were: pool-run guild N = 388, poolcover guild N = 830, and available N = 3176. Suitability values were based on the significance of the Strauss linear index values calculated

Overall the riffle guild prefers shallow, fast water with low embeddedness, cobble sized substrate and nearby cover. The fast generalist guild prefers locations with medium depths and velocities, cobble to boulder-sized substrate, low embeddedness and nearby cover. The pool-run guild prefers locations with deeper depths, medium velocities, cobble to boulder-sized substrate, low embeddedness and nearby cover. The pool-cover guild prefers deeper, slower water with embedded substrate and nearby cover.

DISCUSSION

The lessons learned during this study focus mainly on ways to include the elements of fish habitat diversity into habitat criteria: (1) variables other than depth, velocity and substrate are important to habitat choice in species, (2) data can be gathered on multiple species at a time without much more effort than gathering data on one species, (3) habitat guild structures can work in other systems, (4) guild criteria can be created without any more effort than creating species criteria and (5) Strauss linear index appears to provide a reasonable approach for developing criteria for categorical variables.

Traditional habitat analysis has focused on a few individual variables such as depth, velocity and substrate. Habitat suitability criteria have traditionally been developed for individual variables separately and then the habitat is evaluated based on a combination of these independently developed criteria. Recent work has tried to move away from the individual variable approach to include complex hydraulic variables because species make habitat choices based on multiple factors at the same time (Brooks et al., 2005; Lamouroux and Jowett, 2005). Froude number was used to address multiple aspects of a species' habitat choice with one variable. Froude number is a complex hydraulic variable that accounts for depth and velocity simultaneously; therefore, it may demonstrate a species' habitat selection more accurately than either depth or velocity individually. Previous work has found the Froude number was significantly related to macroinvertebrate abundance (Brooks et al., 2005) and reach habitat value (Lamouroux and Jowett, 2005; Schweizer et al., 2007). Similarly, our study supports the importance of Froude number for discriminating between fish habitat guilds.

Distance to cover, although traditionally not examined in fish habitat studies, may also be an important habitat variable. Multiple studies have found that trout and salmon species select habitat closely related to cover although they showed no preference between cover types (Quinn and Kwak, 2000; Banish et al., 2008; Holecek et al., 2009). Additionally, while many fish species do not spend much time actually using cover they often remain near cover in case they need to use it (Groshens, 1993). Because of the way distance to cover was measured in this study, criteria were developed using both tolerance limits and the Strauss index. The two methods resulted in different criteria. The differences in the results are a cause for concern and warrant further investigation into the correct approach for evaluating distance to cover. Tolerance limits will probably result in the most accurate criteria for distance to cover as long as enough distance is considered when measurements are taken.

By including variables such as Froude number and distance to cover, a more complete analysis of habitat selection was developed with little additional time spent in the field. Because species select habitat based on a range of variables it is important to include multiple habitat variables and variables that combine multiple aspects of the habitat, such as Froude number, so that criteria represent a more realistic picture of how species and guilds select habitat. While distance to cover remains a cumbersome variable to incorporate into one-dimensional models such as PHAB-SIM, the development of two-dimensional models has made it easier to account for distance to cover in physical habitat analysis studies. Furthermore, advances in two-dimensional





Figure 7. Habitat criteria for embeddedness. The guild bars represent the frequency that the embeddedness category was used by members of the guild and the available bars represent the frequency that embeddedness was found in all sampled locations in the North Fork Shenandoah River. The number of observations used were: riffle guild N = 338, fast generalist guild N = 351, pool-run guild N = 194, pool-cover guild N = 415, and available N = 1588. Suitability values were based on the significance of the Strauss linear index values calculated

modelling make it possible to incorporate spatially explicit variables in habitat analysis (Crowder and Diplas, 2006; Shen and Diplas, 2008).

Typically instream flow studies examine just one or two species; however, if these studies are going to provide useful information for making decisions in stream systems with diverse fish communities then criteria development needs to look at the entire aquatic community (Orth, 1987; Braaten and Berry, 1997). Collecting field data on multiple species requires relatively little extra effort than data collection for a few specific species. This is particularly true of the guild approach which relies on the collective data for all species in a guild, thus reducing the amount of data needed for any particular species.

A guild approach is most useful if the guilds are transferable from one river system to another with only minor modifications. This study took a guild structure previously established for the Roanoke River, Virginia (Vadas and Orth, 2000) and modified it for use on the North Fork Shenandoah River, Virginia. Initial modifications were made to the guild structure to account for different species

between the two rivers. After initial species placement into the guilds, no species were moved despite some species having a higher percentage of their data in guilds other than the one they were assigned to. This was done because the guilds themselves were different from each other and any species movement would automatically change the definitions of the guilds. This could lead to endless changes as the guilds were constantly redefined each time a species was moved; therefore, the species were all left in place. The results of this study confirmed that the four guilds were significantly different from each other in another river; therefore, the habitat guild structure used in one river system was successfully applied, with minor modifications, to another river system. While transferring a guild structure between two river systems with similar fish communities worked for this study, more research is needed to determine if a guild structure can be applied to a wider range of systems successfully.

The process for creating guild criteria was identical to that used in creating single species criteria, except data from multiple species were combined into a single set of criteria.



Figure 8. Habitat criteria for cover. The X-axis categories are cover presence or absence. The guild bars represent the frequency that cover was present or absent at guild locations and available bars represent the frequency that cover was present or absent in all sampled locations in the North Fork Shenandoah River. The number of observations used were: riffle guild N = 338, fast generalist guild N = 351, pool-run guild N = 194, pool-cover guild N = 415, and available N = 1588. Suitability values were based on the significance of the Strauss linear index values calculated



Figure 9. Comparison of habitat criteria created using nonparametric tolerance limits and distance groupings using Strauss linear index values. Line width gradients are the 100% suitable (thickest line), 50% suitable (medium line), and 20% suitable (thinnest line)

The HSC were created using all the data for every species assigned to the guild. When multiple species assigned to the same guild shared a common data point, that data point was only counted one time when creating the criteria. The main issue surrounding the development of guild criteria involves how each species was included in the guild criteria. In this study every data point collected for every species was included in the final guild criteria. As a result, the most common species were weighted more heavily than rare species. A way to counteract the effect of common species would be to weight all species equally in the guild criteria. The problem with this approach is getting enough data points for rare species. In some cases we were only able to get one or two observations for a species such greenside darter (Etheostoma blenniodies) in the riffle guild or bull chub (Nocomis ranevi) in the fast generalist guild. That means these species made little contribution to the guild criteria, which could be problematic if they are important species such as a threatened or endangered species. The best approach for dealing with rare species when developing guild criteria needs further study.

Nonparametric tolerance limits were used for creating habitat suitability criteria for the continuous variables for several reasons. Tolerance limits provide a consistent and repeatable way to create criteria when compared to the more arbitrary nature of curve fitting techniques (Newcomb *et al.*, 1995). With tolerance limits anyone can take the same data set and create identical criteria. The use of the Strauss linear index also provided a consistent and repeatable method for creating criteria for categorical habitat variables. The Strauss index is a statistical method for evaluating the ratio of per cent categorical variable utilization to its availability in the environment (Strauss, 1979). The use of this index reduces some of the subjectivity often associated with substrate and cover criteria development.

Guild-based criteria development may improve the ability of habitat suitability criteria to represent the habitat needs of a diverse aquatic community. If fish habitat guilds are used in conjunction with habitat guilds for stream macroinvertebrates and other species groups then for the first time instream flow studies might come close to accounting for the habitat requirements of the entire aquatic community (Gore *et al.*, 2001; Orth and Newcomb, 2002).

This research represents the first attempt to test habitat guild typology in another river basin. The results indicate that there is potential for guilds to transfer between stream systems. Additionally, the study results suggest several methods for including habitat diversity into fish habitat criteria. Variables, such as Froude number, combine multiple aspects of the habitat in order to represent species habitat choices. Though much research is needed to determine the best way to use a habitat guild approach in developing habitat suitability criteria in a stream system, the approach appears to have some definite benefits for studies melding hydrodynamic models to habitat needs for fish assemblages. Further work is needed to test guild structures and their associated criteria in other rivers, the transferability of guilds between river systems, and the best approach to including rare species into habitat guilds.

ACKNOWLEDGEMENTS

The authors would like to thank the numerous individuals who contributed to this study including T. Newcomb, C. A. Dolloff, D. Hayes, J. Krstolic, S. Reeser, J. Kauffman, J. Milam, J. Harris, C. Holbrook, L. Scarbourgh, V. Eaton, M. Anderson, J. Kilpatrick, T. Smith and M. Chan. They would also like to thank the NFSR basin landowners who allowed them access to the study sites. Funding for this study was provided by the Northern Shenandoah Valley Regional Commission and the Virginia General Assembly. They are grateful to Ken Bovee and one anonymous reviewer whose insightful comments helped improve this paper.

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