*Transactions of the American Fisheries Society* 130:217–235, 2001

# Formulation of Habitat Suitability Models for Stream Fish Guilds: Do the Standard Methods Work?

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*Abstract.*—Habitat suitability index (HSI) models for seven fish guilds in two segments of the upper Roanoke River drainage, Virginia, were formulated for the summer seasons of 1989 and 1990. We considered five habitat variables as potential limiting factors: depth, average and demersal velocities, average substratum size, and percent cover. These physical variables were modeled both separately and as composite HSI indices. Composite models were built from linear regression equations (both simple and multiple) in which the observed guild density in quadrats was regressed against physical microhabitat variables or individual suitability indices (SIs = predicted fish densities). There were five major findings. First, habitat variables were used independently by most fish guilds, as statistical interactions were weak and inconsistent for regression models predicting guild densities from physical variables. That is, fish-microhabitat relations for target habitat variables were typically unaffected by the condition (value) of other habitat variables. Although polynomial (curvilinear) terms were stronger than interaction terms, linear terms accounted for most of the variation in guild densities among quadrats. Second, the predictive power of these complex physical models for guild densities was matched by that of multiplying the SIs for individual microhabitat variables together. Third, this product (joint-suitability-factor) approach was superior to other methods of developing composite HSIs from individual SIs because it was consistently accurate across fish guilds (owing to the lack of strong statistical interactions) and was a simpler regression model (involving only one slope coefficient). Fourth, observed guild densities for each river segment were well correlated with those predicted by the product equation with SI data from the other river segment, thus cross-validating our HSI models in the upper Roanoke River drainage. Fifth, maximum guild densities for habitat variables that were stratified into a few or several categories provided useful indices of the limiting factors for fish guilds because higher densities indicated greater habitat specialization. Across all guilds, depth was consistently the most important factor in habitat selection. In sum, our results suggest that fish-habitat statistical interactions are not strong enough to invalidate the product equation traditionally used by fish researchers to build composite HSI models, at least when SI data are aggregated by habitat use guild.

Habitat suitability index (HSI) models have often been used to characterize habitat availability for salmonids and other freshwater and estuarine fishes, usually for the purpose of predicting human impacts on aquatic ecosystems (Terrell 1984; Bovee 1986; Rubec et al. 1999; Brown et al. 2000). For example, micro-HSI models have often been interfaced with microhabitat data collected at different flows to predict changes in fish habitat availability resulting from flow changes (Bovee 1986). Verbal, mathematical, or graphic summaries of habitat use data can be translated into a standardized code for use in predictive HSI models (Schamberger et al. 1982).

Although suitability index (SI) models are usually created separately for different microhabitat variables (e.g., cover, substratum size, depth, and velocity), these SIs need to be coalesced if lotic biologists are to accurately predict changes in overall habitat availability at different flows (Terrell 1984; Bovee 1986) and streamline sampling programs to estimate population sizes (Statzner et al. 1988, 1998). Most researchers multiply the SIs for individual habitat variables together (the ‘‘product equation’’) to obtain a composite HSI (Bovee 1986); the model is also known as the incremental or joint-suitability-factor method (Morin et al. 1986; Jowett and Richardson 1990; Statzner et al. 1998). But this method is based on the assumption that fish select particular habitat variables independently of others (Bain et al. 1982; Bovee 1986; Scott and Shirvell 1987), as multiplication of individual SIs is analogous to multiplying probabilities together (Remington and Schork 1985).

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Received October 28, 1999; accepted August 4, 2000

There are several alternative aggregative indices for combining habitat variables. Because they employ different assumptions, they can lead to different estimates of habitat availability and thus to divergent management strategies to protect fish and wildlife resources (Gan and McMahon 1990; Van Horne and Wiens 1991). Several of these indices involve the addition or multiplication of individual SIs. The arithmetic-mean HSI assumes that good habitat conditions on one axis (e.g., cover) can compensate for poor conditions on another axis (e.g., depth) (Terrell 1984; Bovee 1986). The geometric-mean HSI is the *n*th-root of the product of *n* habitat variable indices (e.g., the fourth root of the product of four indices). This approach also implies some compensation (i.e., interdependent selection of habitat variables; Gan and McMahon 1990; but see Rubec et al. 1999), yet like the product equation, it yields zero suitability when any habitat variable is unsuitable (Brown et al. 2000). The weighted product equation involves assignment of an exponent to each SI before multiplication to reflect the particular importance of each habitat variable to the fish (Leclerc et al. 1995).

Several other aggregative methods also exist, many of them regression based. The lowest individual SI, when used as the composite HSI, assumes that the worst habitat axis solely determines fish abundance (Terrell 1984; Bovee 1986). Multiple-regression equations that use physical habitat variables rather than SIs to calculate composite HSIs often include polynomial (Gore 1989) or interaction terms when aquatic animals are known or believed to select habitat variables nonlinearly or interdependently. This approach has been used extensively in North America (Gore and Judy 1981; Orth and Maughan 1982, 1983; Morin et al. 1986) and New Zealand (Jowett and Richardson 1990; Jowett et al. 1991), including in recent bioassessments of stream habitat mitigation (Gore and Hamilton 1996; Gore et al. 1998). Interactive assessment models are regression equations that incorporate biotic variables (e.g., the densities of invertebrates and fishes) as well as physical habitat equations. This approach can improve predictions of density, growth, and other population parameters (Malmqvist 1980; McClendon and Rabeni 1987; Emlen et al. 1992) when competitive or predatory impacts are significant (Brown et al. 2000). The interactive-stratified approach is another method of accounting for interdependent habitat selection, in that one habitat variable is stratified to generate separate SI curves for another habitat variable (Bovee 1986). Finally, turbulence (complex hydraulic) variables such as Froude, Reynolds, and boundary Reynolds numbers, which include depth, velocity, or substratum variables in combination (Vadas and Orth 1998), can also reduce the analytical problems from statistical interactions among simple variables (Statzner et al. 1988, 1998; Heede and Rinne 1990; Wetmore et al. 1990) by minimizing model complexity and propagation of error (Gore 1989).

In essence, these aggregative equations are verification rather than validation techniques (see Farmer et al. 1982; Terrell 1984) because they use single data sets to assess the internal consistency of composite HSI models. Although such verification involves self-correlation, the equations can be validated for robustness by being used to predict animal density or relative abundance at other relevant sites or times (Marcot et al. 1983; Morin and Peters 1988; Rubec et al. 1999; Brown et al. 2000).

Finally, although most HSI models are built for individual fish species, it is also possible to build models for habitat use guilds. The latter, larger-scale approach has several advantages: (1) SI curves should be less variable (i.e., more realistic in breadth) owing to larger sample sizes (Fausch et al. 1988); (2) more of the available fish assemblage is considered, which will lead to better protection of stream ecosystems; (3) fewer HSI models need to be interfaced with habitat-flow data; and (4) individual species may fluctuate more via biotic and abiotic factors than whole guilds, making predictions of fish density more difficult than that of guilds in the face of habitat changes (Orth 1995; Vadas and Orth 2000). Indeed, Morin and colleagues (Morin et al. 1986; Morin and Peters 1988) found higher predictive power for the overall abundance of blackflies *Simulium* sp. ($R^2 = 10$–58%, median 42%) than for individual blackfly species ($R^2 = 26.5\%$) in Quebec streams based on polynomial regression equations of physical habitat variables. Other researchers have taken even broader approaches, developing HSIs for the total standing crop of fish assemblages (Layher and Brunson 1992) or the species diversity of aquatic-macroinvertebrate assemblages (Orth and Maughan 1983; Gore and Hamilton 1996; Gore et al. 1998).

This paper addresses these issues in the drainage of the upper Roanoke River (URR), a small river in southwestern Virginia with cool- to warmwater, with particular emphasis on the degree to which fish guilds use habitat variables interdependently. We break with tradition by building fish-habitat

TABLE 1.—Species richness and important mesohabitats of the seven habitat-use guilds developed by Vadas and Orth (2000). Letters in parentheses represent categories of species in decreasing order of abundance: dominant (D), subdominant (S), common (C), typical (T), uncommon (U), and rare (R); see Vadas and Orth (1997). Underlined categories represent the most abundant species in each guild.

| | | Species richness of fish and frog families | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Superguild and guild | Important habitat(s) | Minnows | Darters | Suckers | Cat-fishes | Sunfishes | Scul-pins | Tad-poles |
| Rheophiles | | | | | | | | |
| Fast riffle | Fast riffles | 0 | 1 (S) | 1 (T) | 1 (T) | 0 | 0 | 0 |
| Riffle–run | Riffles and runs | 1 (C) | 2 (D, S) | 0 | 0 | 0 | 1 (T) | 0 |
| Fast generalist | Riffles and runs more than pools | 1 (D) | 1 (T) | 2 (C, T) | 1 (D) | 0 | 0 | 0 |
| Shallow rheophilic | Shallow pools and slow riffles | 2 (U) | 0 | 0 | 0 | 0 | 0 | 0 |
| Limnophiles | | | | | | | | |
| | | | | | 0 | | | |
| Pool–run | Pools and runs | 4 (S, 2C, T) | 0 | 1 (U) | 0 | 0 | 0 | 0 |
| Open pool | Pools regardless of cover levels | 2 (T) | 0 | 0 | | 0 | 0 | 0 |
| Pool cover | Pools with cover | 2 (T, U) | 1 (R) | 4 (R) | 1 (R) | 3 (2T, R) | 0 | 1 (R)[a] |

[a] Unidentified *Rana* (frog) larvae.

models for guilds rather than for individual species or life stages and by using guild densities rather than normalized abundance data that equalize the maximum SIs of habitat variables. Whereas individual SIs are based on histograms of observed (average) guild density by habitat condition, composite HSIs are developed from regression equations that reflect physical factors (e.g., velocity) or individual SIs for such factors (e.g., guild density for a given velocity condition) as predictor variables. Linear regression equations are compared for their ability to predict guild abundance in a given quadrat or mesohabitat type (i.e., a set of quadrats with similar physical conditions). Finally, HSIs developed from the product equation for two URR segments are cross-validated with each other to test HSI usefulness with independent data sets (Scott and Shirvell 1987; Shirvell 1989b; Statzner et al. 1998).

## Methods

*Field work.*—Methods for collecting fish and sampling habitat, as well as descriptions of the sample sites, are presented elsewhere (Vadas and Orth 1993, 1997, 1998). Briefly, four to six macrohabitat sites were sampled in the summer (low-water) seasons of 1989 and 1990 in the lower South Fork (LSF) and upper main stem (UMS) of the Roanoke River (Montgomery and Roanoke counties). This involved both seining and electroshocking to efficiently collect rheo- and limnophilic fishes (Bart 1989) and tadpoles in quadrats (typically 20–50 $m^2$ in size), along with measurement of habitat variables within those quadrats. Habitat variables included depth, average velocity, demersal velocity (4.5 cm above the bottom), and average substratum size (coded 1–9 from mud to bedrock) at three points in each quadrat (Aadland 1993; Freeman et al. 1997), and percent cover (organic or anthropogenic) relative to the benthic area of each quadrat. Altogether, 615 quadrats were sampled.

*Formulation of habitat use guilds and SI models.*—We developed habitat use guilds for regularly collected species that differed in mesohabitat use (Table 1) based on univariate and multivariate analyses of species similarity for nonfry life stages (Vadas and Orth 1997, 2000). We formulated SI models for these guilds by plotting average densities versus the habitat categories; our approach was similar to those of Bain et al. (1982) and Rubec et al. (1999) but without the normalization of data to the range 0 to 1 (Layher and Brunson 1992). That is, we did not divide guild densities by maximum abundance, as such normalization unrealistically gives equal weight to habitat variables (Brown et al. 2000) that often differ in their importance to fish (Leclerc et al. 1995). Analyses were done separately for the LSF and UMS, but data for the two years were pooled to increase sample sizes. With respect to the densities, we preferred mean to median values (Moyle and Lound 1960) because the latter were often zero as a result of there being no guilds in some quadrats with suitable habitat (Vadas and Orth 1997, 2000; see also Maravelias 1999).

*Unpooled quadrat (microhabitat) regression analyses.*—Four verificatory, multiple-regression

TABLE 2.—Multiple-regression equations to predict the density (fish per 100 $m^2$) of fish habitat-use guilds ($HSI_i$) in a given quadrat from four microhabitat variables: $C$ = cover (%), $S$ = average substratum size (1 to 9), $D$ = depth (cm), $V$ = average water column or demersal velocity (cm/s). Variables $X$, $Y$, and $Z$ are generic variables that are used to illustrate the form of each equation. Intercepts were excluded from the models.

| Equation | Form of explanatory variables |
|---|---|
| M1. $\mathrm{HSI}_i = (B_C \cdot C) + (B_S \cdot S) + (B_D \cdot D) + (B_V \cdot V) = \sum B_X \cdot X$ | Linear |
| M2. $\mathrm{HSI}_i = \sum B_X \cdot X + \sum B_Y \cdot X^2 + \sum B_Z \cdot X^3$ | Linear and polynomial |
| M3. $\mathrm{HSI}_i = \sum B_X \cdot X + \sum B_1 \cdot XY + \sum B_2 \cdot XYZ + \cdots$ | Linear and interaction |
| M4. $\mathrm{HSI}_i = \sum B_X \cdot X + \sum B_Y \cdot X^2 + \cdots + \sum B_1 \cdot XY + \cdots$ | Linear, polynomial, and interaction |

models (Draper and Smith 1981; SAS 1985) were built to predict guild densities in individual quadrats; these were based on several physical habitat variables (Table 2) that were shown to be independent of each other in multivariate-similarity (factor) analyses (Vadas 1994). Separate analyses were done for the two river segments (LSF and UMS) and for average versus demersal velocity to examine the robustness of the regression models at such quadrat resolution. The models included coefficients for linear terms (M1), linear and polynomial terms (M2), linear and interaction terms (M3), and all three types of terms (M4). We examined tolerance values (SAS 1985) to determine the degree of multicollinearity (interdependence) among predictor variables.

We also set the $y$-intercepts equal to zero because fish should be absent from unsuitable quadrats (Orth and Maughan 1983; Bovee and Zuboy 1988), although this caused a redefinition (enhancement) of statistical significance and the coefficients of determination (values of $R^2$), as Bourgeois et al. (1996) also found. Although Bourgeois et al. (1996) deemphasized the satisfactory predictive power of verificatory regression analyses without intercepts, this stemmed from their lack of data points (HSIs and densities) of low value. In our data set, by contrast, there was a plethora of zero densities and HSIs, the latter resulting from the frequent absence of fish guilds from extreme habitat (especially hydraulic) conditions (Figures 1, 2). We compared our URR equations by examining adjusted-$R^2$ values (Fausch et al. 1988), that is, the percentages of variation explained by the regressions after correcting for the number of predictor variables (SAS 1985), as most regressions were very highly significant ($P \leq 0.001$).

We also performed verificatory linear-regression analyses with the product equation (Table 3), to predict guild densities in each quadrat and river segment using nonnormalized SIs (guild densities) for individual microhabitat variables (Figures 1, 2). The product regressions were separately analyzed by means of few-category and several-category SI data sets (Table 4). These class criteria were based on the physical values that best segregated fish habitat use guilds, which often yielded unequally sized categories for a given habitat variable (Vadas and Orth 2000). Hence, there were two to three classes for the few-category analyses, with sample sizes ranging from 37 to 249 quadrats for each habitat category. Likewise, there were five to eight classes for the several-category analyses, with sample sizes ranging from 13 to 214 quadrats per habitat category. Intercepts again were excluded from the models for both theoretical and empirical reasons.

We did not transform guild density data because there were too many quadrats lacking a given guild (or fish species) for Gaussian (''normal'') distributions to be generated by any means (see Maravelias 1999). We did, however, undertake further analyses using pooled quadrat data to minimize the analytical problems from outliers and other statistical violations.

*Pooled-quadrat (mesohabitat) regression analyses*.—Pooled-quadrat regressions were done on mean guild densities (SIs) across mesohabitat types to develop composite HSIs. That is, we ran several simple- and multiple-regression analyses with mesohabitat (pooled-quadrat) resolution data (Table 3), which reduced sample sizes and probably increased normality via the central-limit theorem (Remington and Schork 1985). We further minimized the influence of undersampled habitat types in two ways. First, we used the WEIGHT statement in SAS (1985), which prevented pseudoreplication via sample size enlargement (Hurlbert 1984). Second, we reran the product equation (D1 in Table 3) without habitat types of $N = 1$ to see if outlying guild densities (based on single quadrats) were adversely affecting the regression equations (Fausch et al. 1988).

There were six such verification analyses. The equations included the (1) product equation (D1), which assumes that fish select habitat variables independently; (2) the geometric-mean (D2) and sum equations for one (D3) and multiple (D4) slopes, which all assume that good conditions along one habitat axis compensate for poor conditions along another; (3) the high-low equation (D5), which assumes that fish are most affected by the best or worst habitat variables; and (4) the guild equation (D6), which assumes that the density of a guild can be predicted from the HSIs (densities) of all other guilds. The latter equation was similar to the interaction assessment model of Emlen et al. (1992) but without terms for physical habitat variables or invertebrate foods. We evaluated these various models by examining adjusted-$R^2$ values and the significance of individual slopes in the multiple-regression equations. Intercepts again were excluded from the models for theoretical and empirical reasons.

We also validated the product equation (D1) by using individual SIs generated from one river segment to predict composite HSIs in the other segment, that is, we performed two cross validations (LSF-UMS and UMS-LSF). Adjusted-$R^2$ values would be expected to remain high if fish guilds had SI curves of similar shape in the two river segments, even if absolute densities were higher in one segment.

All pooled-quadrat regressions were done with few habitat categories, as sample sizes were too small when several categories were used. That is, the few-category analysis yielded 54 possible and 49 actual habitat types (Vadas 1994), the latter a significant fraction of the total number of quadrats available in LSF and UMS (Table 5).

## Results and Discussion

### *Composition of Habitat-Use Guilds*

Except for the fast-riffle, riffle-run, and pool-run guilds, the guilds were dominated by multiple species (Table 1). Whereas the fast-riffle and riffle-

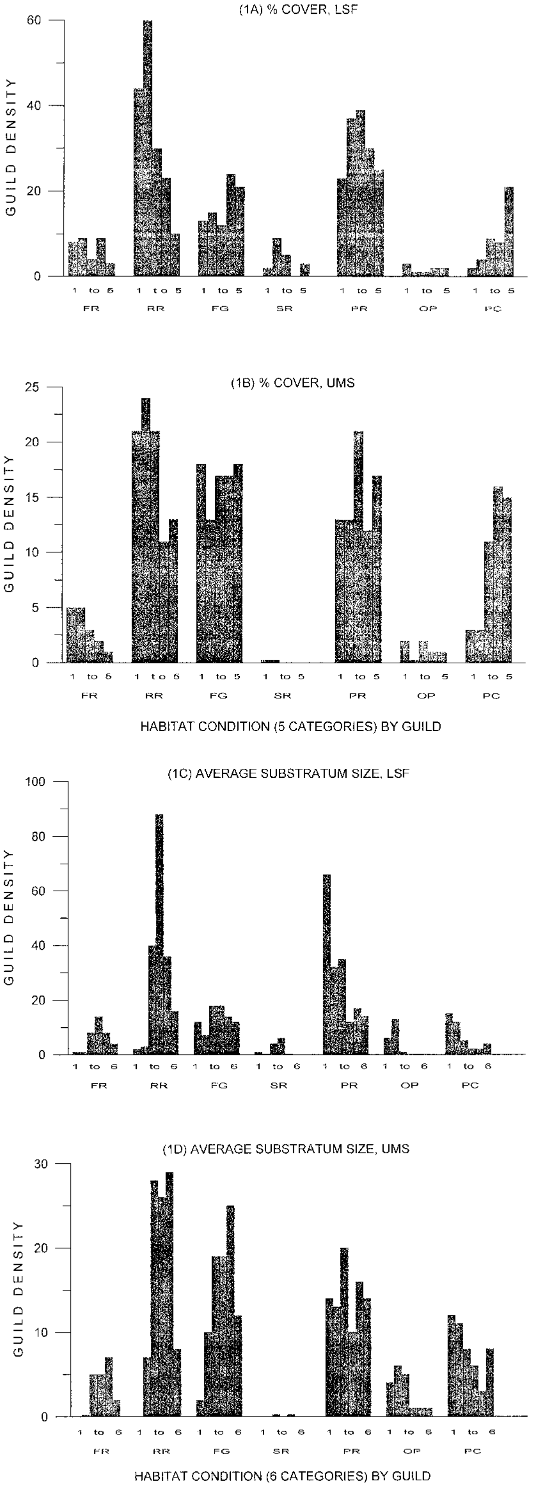

FIGURE 1.—Suitability index histograms for fish in the lower South Fork (LSF) and the upper main stem (UMS) of the Roanoke River during 1989–1990 using several

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mesohabitat categories for two bottom-topographic variables, (**1A, B**) percent cover and (**1C, D**) average substratum size (see Table 4). Densities are numbers of fish per 100 m$^2$ for a given habitat category. Guilds are abbreviated as follows: FR = fast riffle, RR = riffle-run, FG = fast generalist, SR = shallow rheophilic, PR = pool run, OP = open pool, and PC = pool cover. Note the different scales of the density ($y$) axes.

run guilds were dominated by darters, minnows were prominent in the shallow-rheophilic, pool-run, and open-pool guilds. In contrast, the fast-generalist and pool-cover guilds consisted of several important fish families, the latter guild being particularly species rich. Other north-temperate ichthyologists have also found relatively high biodiversity in stream habitats with organic cover (Angermeier and Karr 1984; Benke et al. 1985; Thevenet and Statzner 1999).

### *SI Plots for Individual Habitat Variables*

SI histograms with several categories for cover, substratum size, depth, and average velocity are shown in Figures 1 and 2 for the two river segments separately. Although these plots are more jagged than SI histograms with fewer habitat categories (Vadas 1994), the several-category plots offered more precise resolution of fish habitat preferences and usually lacked major bimodality. Together, these plots showed that the fast-riffle and riffle-run guilds used the lowest cover levels, whereas the pool-cover guild used the highest cover levels. Rheophiles selected midsize substrata and shallow water, with the riffle-run and shallow-rheophilic guilds preferring the shallowest depths. In contrast, limnophiles selected finer substrata and medium or deep water, although these three guilds selected coarser substrata in UMS (in association with the greater availability of large rocks) than in LSF (Vadas and Orth 1998, 2000). Moreover, the pool-cover guild showed consistent, major bimodality in the several-category analysis because of its association with large rocks when other ''cover'' was unavailable in both river segments (our personal observations, 1989–1991). Whereas the fast-riffle guild was most abundant in the fastest microhabitats, other rheophiles were predominant in medium-velocity flows. In contrast, the pool-run and open-pool guilds selected medium or slow microhabitats, whereas the pool-cover guild was most abundant in slow water.

These results suggest four conclusions. First, individual guilds used habitat similarly in the two river segments, although some guilds showed minor shifts in their SI plots. Second, the seven guilds

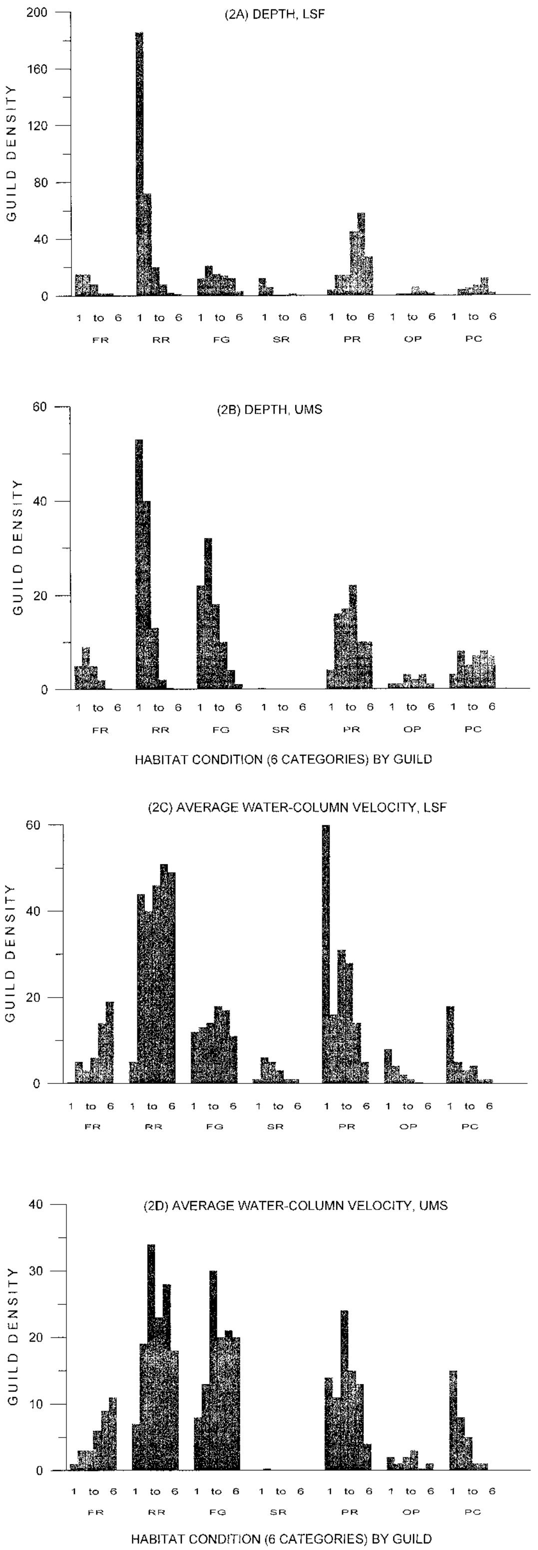

FIGURE 2.—Suitability index histograms for fish in the lower South Fork (LSF) and the upper main stem (UMS) of the Roanoke River during 1989–1990 using several mesohabitat categories for two hydraulic variables, (**2A, B**) depth and (**2C, D**) average velocity in the water column. See Figure 1 for further details.

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TABLE 3.—Verificatory regression equations without intercepts to predict the density of fish habitat-use guilds ($HSI_i$) in a given quadrat (equation D1) or mesohabitat type (equations D1 to D6). The $SI_x$ variables are the expected (mean) densities of a given guild under given habitat conditions; $SI_H$ and $SI_L$ are the $SI_x$ variables with the highest and lowest values, respectively; and the $HSI_y$ variables are the expected (mean) densities of all other guilds under given habitat conditions. See Table 2 for other abbreviations.

| Equation | Equation type |
|---|---|
| D1. $HSI_i = B_p \cdot (SI_C \cdot SI_S \cdot SI_D \cdot SI_V) = B_p \cdot \Pi SI_x$ | Product |
| D2. $HSI_i = B_g \cdot \prod SI_x^{0.25}$ | Geometric mean |
| D3. $HSI_i = B_o \cdot \sum SI_x$ | One-slope sum |
| D4. $HSI_i = \sum B_m \cdot SI_x$ | Multiple-slope sum |
| D5. $HSI_i = (B_H \cdot SI_H) + (B_L \cdot SI_L)$ | High–low |
| D6. $HSI_i = \sum B_y \cdot HSI_y$, where $y \neq i$ | Guild association |

were reasonably distinct from each other when all habitat variables were considered (see also below) and thus more accurately represent fish habitat use than the traditional classification of fish as ‘‘pool,’’ ‘‘run,’’ or ‘‘riffle’’ species (Vadas and Orth 1998, 2000). Third, although robust HSI models are often harder to build for habitat-generalized fishes, at least at macrohabitat scales (Layher et al. 1982; Terrell 1984; Layher and Maughan 1987), broader-niched guilds such as the fast-generalist and pool-run guilds (Vadas and Orth 2000; also see below) yielded reasonably similar micro-SI plots for our two URR segments. And fourth, the bimodal distribution for the pool-cover guild suggests that substratum and cover characteristics are interdependent because fish used protruding large boulders as cover even though they typically selected gravel-cobble substrata in the URR (Vadas and Orth 2000). Similarly, U.S. researchers have collectively found that various fishes, including three of our pool-cover species (smallmouth bass *Micropterus dolomieu,* the northern hog sucker *Hypentelium nigricans,* and the bluntnose minnow *Pimephales notatus*), one pool-run species (the white sucker *Catostomus commersoni*), and one fast generalist (black jumprock *Scartomyzon [=Moxostoma] cervinus*) had bimodal substratum distributions because of preferences for rocky cover (large boulders or bedrock) and finer substrata (Leonard et al. 1986; Todd and Rabeni 1989; Aadland et al. 1991; Groshens and Orth 1993). Such interdependencies among substratum and cover characteristics suggest that the interdependent selection of these variables by our pool-cover guild may be an artifact of measurement deficiencies (see below).

### *Formulation of Composite HSIs from Unpooled-Quadrat (Microhabitat) Data*

Using multiple-regression results to predict guild densities (composite HSIs) in specific quadrats yielded predictions that were more accurate for the three abundant rheophilic guilds (adjusted

TABLE 4.—Categories for microhabitat variables in the few-class (F) and several-class (S) analyses of fish habitat-use guilds. Substratum codes included 3.5 for an equal mix of small and large gravel, 5.0 for small cobble, and 6.5 for an equal mix of large cobble and small boulders (Vadas and Orth 1998, 2000).

| | | Category | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Habitat variable | Analysis | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Cover (%) | F | <5 | ≥5 | | | | | | |
| | S | <2 | 2–4 | 5–9 | 10–14 | >15 | | | |
| Average substratum size (1–9) | F | <5.0 | 5.0–5.9 | ≥6.0 | | | | | |
| | S | <3.5 | 3.5–4.4 | 4.5–5.4 | 5.5–5.9 | 6.0–6.4 | ≥6.5 | | |
| Depth (cm) | F | <30 | 30–64 | ≥65 | | | | | |
| | S | <15 | 15–29 | 30–44 | 45–64 | 65–84 | ≥85 | | |
| Demersal velocity (cm/s) | F | <15 | 15–39 | ≥40 | | | | | |
| | S | <5 | 5–9 | 10–14 | 15–19 | 20–24 | 25–39 | 40–49 | ≥50 |
| Average velocity (cm/s) | F | <20 | 20–59 | ≥60 | | | | | |
| | S | <10 | 10–19 | 20–29 | 30–49 | 50–69 | ≥70 | | |

TABLE 5.—Adjusted coefficients of determination ($R^2$) for regression equations (Tables 2, 3) to predict fish guild densities in given (unpooled) quadrats. Analyses were done by velocity variable (average versus demersal) and Roanoke River segment (lower South Fork [LSF] versus upper main stem [UMS]) for equations using microhabitat variables (M1 to M4) and by velocity variable and number of habitat categories (few or several) for equation D1, which uses suitability indices. All regressions were very highly significant ($P \leq 0.001$) unless otherwise indicated; $P \leq 0.05$*, $P \leq 0.01$** (level of minimum significance). Relatively high adjusted-$R^2$ values for a given guild are underlined. Sample sizes for LSF and UMS were 262 and 353 quadrats, respectively.

| Guild | Habitat predictor variables (equation) | | | | Product equation (D1) | |
|---|---|---|---|---|---|---|
| | Linear (M1) | Polynomial (M2) | Interaction (M3) | All (M4) | LSF | UMS |
| Fast riffle | 35–40 | 37–44 | 37–50 | 37–51 | 30–43 | 42–51 |
| Riffle–run | 35–39 | 51–53 | 40–49 | 54.5–56 | 41–55 | 52–57 |
| Fast generalist | 34–50 | 35–57 | 35–54 | 36–57 | 37–45 | 53–60 |
| Shallow rheophilic[a,b] | 5–6 | 11–12 | 8** | 9–10** | 10–24 | |
| Pool–run | 17–19 | 20–23 | 18–19 | 18–22 | 17–25 | 23–28 |
| Open pool[b] | 4–5** | 8–11 | 4–8[c] | 6–10* | 19–40 | 11–31 |
| Pool cover | 14–28 | 17–39 | 17–38 | 18–42 | 26–35 | 14–15 |

[a] Guild only tested in the upstream river segment (LSF).

[b] Guild considered rare.

[c] Not always statistically significant.

$R^2 = 30–60\%$) than for the limnophiles (Table 5). The guilds that were least abundant, that is, the shallow-rheophilic and open-pool guilds, were less accurately predicted by equations employing microhabitat variables as predictor variables (equations M1 to M4; adjusted $R^2 < 15\%$) than the pool-run and pool-cover guilds (adjusted $R^2 = 15–45\%$). In contrast, the product equation (D1) yielded more similar adjusted-$R^2$ values for the latter four guilds (collective range 10–40%). Table 5 also shows that linear HSI models (M1) provided predictions that were nearly as good as those of models with polynomial or interaction terms (equations M2 to M4). Although both of these latter terms increased the adjusted-$R^2$ values, polynomial terms were usually more influential than interaction terms.

These results suggest two major conclusions. The first is that the use of polynomial or interaction terms for microhabitat variables will probably not greatly improve predictive power over that of the product equation (D1) traditionally used by instream flow researchers (Gore and Judy 1981). Our results correspond to those obtained for rheophilic macroinvertebrates, as the $R^2$ values were comparable with habitat conditions and SIs as predictor variables (Table 6). However, they contrast with the analyses of Orth and Maughan (1982), who found $R^2$ values of 22–71%, with higher values in summer (when habitat was probably more limiting) than in spring. At least with our URR data set, it was valid to select the product equation over more complicated multiple-regression equations because D1 was a more parsimonious descriptor of fish habitat use despite the presence of some significant fish-habitat interactions. Indeed, our

TABLE 6.—Ranges of $R^2$ values for different statistical models to predict the abundance of lotic macroinvertebrates, based on microhabitat data in the literature. The data sets include Morin (Morin et al. 1986; Morin and Peters 1988) for several rheophilic blackfly (simuliid) species, Orth (Orth and Maughan 1983) for invertebrate taxa that were mostly rheophilic, and two Jowett studies (Jowett and Richardson 1990; Jowett et al. 1991) of the rheophillic mayfly *Deleatidium* spp. The symbols I (individual) and S (several) refer to the number of habitat variables that were used for the regressions; underlining indicates relatively high $R^2$ values for a given data set.

| Dependent variable and model types | Morin | Orth | Jowett | |
|---|---|---|---|---|
| | | | 1990 | 1991 |
| Habitat conditions | | | | |
| Linear–I regression | | | 8–33 | |
| Polynomial–I regression | 16–55 | ≤30[a] | 3–24 | ≤35 |
| Polynomial–S regression | 19–64 | | 11–31 | |
| Suitability indices | | | | |
| Product equation | 20–41 | 11–61 | 21–39 | 2–47 |

[a] For hydraulic variables (substratum size gave $R^2 \leq 10$).

multiple-regression equations (M1 to M4) often suffered from multicollinearity (low tolerance), that is, the predictor variables were not independent of each other (our personal observations), so that slope coefficients were biased to compromise comparisons among data sets (Draper and Smith 1981).

The second result is that the densities of lotic taxa in specific quadrats can be predicted with only moderate levels of accuracy by regression equations. This undoubtedly is a result of the wide range of animal densities seen even under apparently optimal habitat conditions (Shirvell 1989a; Jowett and Richardson 1990; Jowett et al. 1991). Perhaps stream fish and invertebrates do not exploit all optimal microhabitats because they are kept below habitat carrying capacity by abiotic disturbances or biotic factors such as predation or they are responding to other, unmeasured abiotic or trophic (food) variables (Shirvell 1986; Orth 1987, 1995; Scott and Shirvell 1987; Gore 1989). Fortunately, this inaccuracy can be reduced when quadrats are pooled into mesohabitat types to increase the spatial scale (see below).

### *Important Habitat Variables in the Unpooled-Quadrat Analyses*

As shown in Table 7, although fish habitat use guilds differed as to the habitat variables that were important, some generalities are apparent. Depth and substratum size were the most consistently important variables, although velocity was especially important for the fast-riffle guild, as was cover for the pool-cover guild. Except for the shallow rheophiles, the more consistently significant variables showed curvilinear responses, reflecting the fact that most guilds peaked at intermediate habitat conditions (Figures 1, 2). Although statistical interaction terms were generally less important than linear and polynomial terms, the pool-cover guild showed a consistently strong cover-substratum-depth interaction. In sum, these results support the adjusted-$R^2$ results of Table 5 in demonstrating the greater usefulness of polynomial terms for most fish guilds. But interaction terms were at least sometimes significant for all guilds except the fast-riffle and shallow-rheophilic guilds.

Several other researchers have also found statistical interactions among habitat variables for pool-cover fishes. First, laboratory research on sunfishes exposed to aquatic cover (Casterlin and Reynolds 1978; Angermeier 1992) and brook trout *Salvelinus fontinalis* exposed to shade (overhead) cover (Gibson and Power 1975; Gibson 1978) demonstrated that fish show greater abundance or feeding success in shallower water when cover is present, presumably because deeper water is itself a form of cover against terrestrial predators (Power 1987). Indeed, when cover is more common away from than near shore, redbreast sunfish *Lepomis auritus* may select deeper nesting sites, as evident in comparisons of the North Anna River with other Virginia streams (Lukas and Orth 1993). Second, smallmouth bass showed depth-velocity interactions in one of two Virginia streams studied by Groshens and Orth (1993) and cover-velocity interactions in the laboratory experiments of Haines and Butler (1969), the latter reflecting the importance of cover in protecting fish from both bright light and high velocities. Groshens and Orth’s (1993) results reflect the preferences for greater velocity in deep water in the North Anna River, although depth did not affect bass velocity use in Craig Creek.

Statistical interactions among habitat variables have also been demonstrated for rheophilic fishes and insects. Studies of juvenile Atlantic salmon *Salmo salar* showed a depth-cover interaction similar to that of brook trout in Gibson’s laboratory experiments (Gibson and Power 1975; Gibson 1978). In addition, studies of three fish (Orth and Maughan 1982) and five zoobenthic species (Gore and Judy 1981) showed significant depth-velocity interactions in inland western U.S. streams. For example, freckled madtoms *Noturus nocturnus* and caddisflies *Nectopsyche lahontanensis* often selected higher velocities in deeper habitats, whereas a minnow (the central stoneroller *Campostoma anomalum*) in our riffle-run guild showed extensive interactions among depth, velocity, and substratum variables during summer (Orth and Maughan 1982; Gore and Judy 1981). The rheophilic mayfly *Deleatidium* spp. selected higher velocities over coarse substrata in the New Zealand river studied by Jowett and Richardson (1990).

These results from the literature collectively suggest that cover-depth and cover-velocity interactions should be common for pool-cover fishes, whereas depth-velocity, substratum-depth, and substratum-velocity interactions should be important for rheophilic animals. Although these results contrast with our URR results, interactions among bottom-topographic and depth variables were apparent for our pool-cover guild.

Nevertheless, the cover-substratum-depth interaction for our pool-cover guild may have been consistently significant because of deficiencies in our cover classification rather than because of bi-

TABLE 7.—Significant habitat variables for multiple-regression equations to predict the density of fish guilds from habitat conditions. Equation types and variables are defined in Table 2; variables may enter equations as linear, polynomial, and/or interaction terms, the last being indicated by multiple letters. Minimum and maximum significance levels (if different) are separated by a slash; $P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***. The row marked ''Sum'' summarizes the important habitat variables for each guild, indicating where there is significant curvilinearity (Curv); underlining indicates the most important variable(s). For each guild see Table 5 for $R^2$ values.

| Guild | Equation | Important variables and interactions |
|---|---|---|
| Fast riffle | M1 | $S$ (ns/***), $D$ (***), $V$ (***) |
| | M2 | $D$ (ns/*), $D^2$ (ns/**), $D^3$ (ns/**); $V^2$ (ns/*), $V^3$ (ns/*) |
| | M3 | $V$ (ns/**) |
| | M4 | $V$ (ns/*) |
| | Sum | Velocity (Curv) > depth (Curv) > substratum size |
| Riffle–run | M1 | $S$ (***), $D$ (***), $V$ (ns/***) |
| | M2 | C (ns/**), C$^2$ (ns/**), C$^3$ (ns/**); $S$ (***), $S^2$ (*/***), $S^3$ (ns/***); $D$ (***), $D^2$ (*/***), $D^3$ (ns/***); $V$ (ns/***), $V^2$ (ns/**), $V^3$ (ns/*) |
| | M3 | $S$ (***), $V$ (ns/**); $SD$ (ns/*), $DV$ (ns/*) |
| | M4 | C$^2$ (ns/*), C$^3$ (ns/*); $S$ (ns/*); $D$ (***), $D^2$ (***), $D^3$ (**/***); $V$ (ns/**), $V^2$ (ns/***), $V^3$ (ns/***); $SD$ (ns/**), $DV$ (ns/**), $SV$ (ns/*), $SDV$ (ns/*) |
| | Sum | Substratum size (Curv) and depth (Curv) > velocity (Curv) > cover (Curv) and several interactions among substratum size, depth, and/or velocity |
| Fast generalist | M1 | $S$ (***), $D$ (ns/***), $V$ (ns/***) |
| | M2 | $C$ (ns/***), $C^2$ (ns/**), $C^3$ (ns/*); $D^2$ (ns/**), $D^3$ (ns/**); $V$ (*/***), $V^2$ (ns/**), $V^3$ (ns/**) |
| | M3 | $S$ (***); $SD$ (*), $CV$ (ns/***); $CDV$ (ns/*), $CSV$ (ns/**), $CSDV$ (ns/*) |
| | M4 | $D^2$ (ns/*), $D^3$ (ns/*); $V^2$ (ns/***), $V^3$ (ns/***); $CV$ (ns/**), $CSV$ (ns/**), $CSDV$ (ns/*) |
| | Sum | Depth (Curv), velocity (Curv), and substratum size > cover (Curv) and several interactions among these four variables |
| Shallow rheophilic | M1 | $S$ (**/***), $D$ (**) |
| | M2 | $C^3$ (*), $S$ (*/**), $D$ (*/**) |
| | M3 | $S$ (**/***) |
| | M4 | $D$ (ns/*) |
| | Sum | Substratum size and depth > cover (Curv) |
| Pool–run | M1 | $S$ (ns/***), $D$ (ns/***), $V$ (ns/*) |
| | M2 | $D$ (ns/**), $D^2$ (ns/*); $V$ (ns/*), $V^2$ (ns/*), $V^3$ (ns/*) |
| | M3 | $S$ (ns/***), $D$ (ns/***); $SD$ (ns/*), $DV$ (ns/*) |
| | M4 | $D$ (ns/***), $D^2$ (ns/**), $D^3$ (ns/*); $V^2$ (ns/*), $V^3$ (ns/*); $SD$ (ns/*) |
| | Sum | Depth (Curv) > velocity (Curv) > substratum size and some interactions among substratum, depth, and/or velocity |
| Open pool | M1 | $D$ (*/**) |
| | M2 | $C$ (ns/*); $S$ (ns/*), $S^2$ (ns/*), $S^3$ (ns/*) |
| | M3 | $D$ (**), $SD$ (ns/*) |
| | M4 | $S$ (ns/**), $S^2$ (ns/**), $S^3$ (ns/*) |
| | Sum | Substratum size (Curv) and depth > cover and substratum–depth interaction |
| Pool cover | M1 | $C$ (*/***), $S$ (ns/***), $D$ (ns/***), $V$ (***) |
| | M2 | $C$ (ns/**); $S$ (ns/**), $S^2$ (ns/*); $V$ (***), $V^2$ (*/**), $V^3$ (ns/**) |
| | M3 | $C$ (ns/**), $S$ (ns/***), $D$ (ns/***); $SD$ (**/***), $DV$ (ns/**), $CS$ (ns/*), $CD$ (ns/*), $CSD$ (*/**), $SDV$ (ns/**) |
| | M4 | $C$ (ns/**), $C^2$ (ns/**), $C^3$ (ns/*); $V^2$ (ns/*), $CSD$ (ns/*) |
| | Sum | Cover (Curv) > velocity (Curv) > substratum size (Curv), depth, and cover–substratum–depth interaction > several interactions among these four variables |

ological behavior. Perhaps our cover and large-rocks variables should have been combined to provide a better cover variable, given that sunfishes often use anthropogenic debris, logs, root wads, boulders, rocky ledges, undercut banks, and aquatic vegetation in the URR (our personal observations, 1989–1991) as well as in other Virginia (Helfrich et al. 1991; Groshens and Orth 1993; Sabo and Orth 1994) and Midwestern streams (Probst et al. 1984; McClendon et al. 1987; Todd and Rabeni 1989; Sowa and Rabeni 1995). This aggregated-cover variable might have shown less incidence of (1) statistical interactions between cover and substratum size and (2) bimodality of substratum SIs. We urge other researchers to combine cover categories into one variable, even if salmonids and warmwater fishes (e.g., sunfishes) do not select all cover types equally (Leonard et al. 1986; Bovee and Zuboy 1988; Todd and Rabeni 1989; Groshens and Orth 1993; Sowa and Rabeni 1995) because the propagation of error with more variables (Gore 1989; Sullivan 2000) and statistical interactions may negate any gains from splitting variables if composite HSIs are to be formulated from the product equation. Indeed, Probst et al. (1984) found that rock bass *Ambloplites rupestris* and smallmouth bass had different depth and velocity preferences in Missouri rivers, depending on the type of cover used by fish (i.e., root wads, suspended logs, or log complexes). Of all the cover variables that Thevenet and Statzner (1999) examined, percent cover best segregated fish species.

Use of simple, general cover variables (e.g., Kinsolving and Bain 1990; Vadas and Orth 1998; Thevenet and Statzner 1999), however, cannot remove all statistical interactions between hydraulic and bottom-topographic variables. For example, ice, turbulence, shallow water, or deep water might provide benthic and pelagic fishes with refuge from terrestrial or aquatic piscivores (Scalet 1974; Casterlin and Reynolds 1978; Gibson 1978; Power 1987) and harsh physical conditions (Gregory and Griffith 1996). Likewise, cobble substrata and benthic depressions may provide refuge for darters (Lee 1977; Leidy 1992), as do boulders and dunes for larger species such as salmonids (Shirvell 1989a; Heede and Rinne 1990) as long as the crevices are wider than the fish when its pectoral fins are extended (Gregory and Griffith 1996). Hence, it is unlikely that all fish species and life stages regard microhabitat conditions equally as potential cover (Wesche 1976; Hamilton and Bergersen 1984). Perhaps qualitative rather than quantitative assessments of cover (O'Neil and Wakeley 1988; Vadas 1994; Rubec et al. 1999; Sullivan 2000) or a more general bottom-topographic variable will be necessary to improve habitat measurement. The latter could include channel roughness, which consists of inorganic, organic, and anthropogenic cover (Gordon et al. 1992), or the boundary Reynolds number, which is a combination of simple-hydraulic and substratum variables (Vadas and Orth 1998); the latter turbulence variable, however, is problematic because habitat availability affected the substratum use of URR limnophiles (present study; Vadas and Orth 2000).

In sum, the search for the Holy Grail of holistic habitat variables has yet to be successful. Given the importance of creating animal-habitat models with simple variables that are easy to measure and manipulate (Marcot et al. 1983; Fausch et al. 1988), coalescence of habitat data into turbulence variables may merely complicate analyses without either providing new information (Statzner et al. 1998; Vadas and Orth 1998, 2000) or enhancing prediction of faunal abundance and biodiversity when the sample size is small (Gore and Judy 1981; Statzner et al. 1988, 1998). Clearly, further research should establish which habitat variables are redundant (O'Neil and Wakeley 1988; Vadas 1994) to minimize confounding HSIs by artificial statistical interactions.

### *Formulation of Composite HSIs: Product Equation*

We further tested the usefulness of the product equation by pooling quadrats with similar microhabitat characteristics into mesohabitat categories. This eliminated noise in the data set and reduced the violation of statistical assumptions, thus enhancing the predictive power of composite HSIs (guild densities in specific habitat types) developed from SIs for individual habitat variables. Table 8 shows that, as with the analyses based on unpooled-quadrat data, the product and other regression equations were most successful for abundant rheophilic guilds and least successful for the rare (shallow-rheophilic and open-pool) guilds. Analogously, Morin and Peters (1988) obtained greater predictive power for meso-level than for micro-level polynomial equations on multiple habitat variables in their attempts to predict overall blackfly abundance in Quebec streams; $R^2$ values were 62–71% at the riffle level and 55% at the rock level.

The product equation (D1) was a consistently good predictor of mean guild densities (Table 8), despite the presence of fish-habitat statistical interactions (Table 7). It was the best equation for predicting the densities of rare guilds, among the best for predicting the densities of the pool-run and abundant rheophilic guilds, and only somewhat inferior to the multiple-slope sum equation (D4) for predicting the density of the pool-cover guild. The geometric-mean equation (D2) rarely performed as well as the product equation, and the single-slope sum equation (D3) never performed as well as the product equation; the guild equation (D6) was clearly inferior to the others for predicting the densities of two limnophilic guilds (the open-pool and pool-cover guilds).

Further analysis of the product equation corroborated the usefulness of this model. First, the adjusted-$R^2$ values for the product equation were increased only slightly by removing undersampled habitat types (Table 8), with little change in slope coefficients. Second, the adjusted-$R^2$ values were similar in analyses treating average and demersal velocity as the velocity variable; the variability of the adjusted-$R^2$ values in Table 8 was usually the result of better predictive power in one of the river

TABLE 8.—Ranges of adjusted-$R^2$ values for each regression equation (Table 3) to predict fish guild densities in given mesohabitat types from suitability index (SI) data. Analyses were done by velocity variable (average versus demersal) and Roanoke River segment (lower South Fork [LSF] versus upper main stem [UMS]) using few-category SIs (equations D1 to D5) or the habitat suitability indices of other guilds in the same mesohabitat types (equation D6). Sample sizes for LSF and UMS were 45–46, compared with 41–44 for mesohabitat types. All values were very highly significant ($P \leq 0.001$) unless otherwise indicated; $P \leq 0.05$*, $P \leq 0.01$** (level of minimum significance). See Tables 2–6 for formats.

| Guild | Product (D1) | | | Geometric mean (D2) | Sum | | High–low (D5) | Guild association (D6) |
|---|---|---|---|---|---|---|---|---|
| | All $N$ | $N \geq 2$[a] | Cross-validated[b] | | 1 slope (D3) | Multiple slope (D4) | | |
| Fast riffle | 64–84 | 70–85 | 60–83 | 61–71 | 60–67 | 71–78.5 | 59–75 | 67–83 |
| Riffle–run | 66–92 | 84–93 | 68–84 | 60–75 | 56–66 | 67–86 | 63–89 | 66–88 |
| Fast generalist | 75–80 | 80–95 | 56–74 | 70–75 | 68–75 | 69–80 | 69–74 | 58–87 |
| Shallow rheophilic[c] | 30–34 | 34–72 | 11–35 | 23–29 | 18–23** | 22–28** | 29–34 | 23–24 |
| Pool–run | 50–78 | 50–88 | 32–42 | 52–70 | 51–69 | 55–69 | 55–70 | 61–75 |
| Open pool | 44–83 | 44–83 | 5–39 | 31–43 | 31–35 | 35–41 | 36–63 | 22–34* |
| Pool cover | 56–62 | 56–62 | 47–65 | 59–63 | 58–61 | 65–72 | 52–70 | 32–42** |

[a] Excluding mesohabitat types represented by only one quadrat.

[b] LSF versus UMS data sets and vice versa.

[c] Except for the cross validations, guild was only tested in the upstream river segment (LSF).

segments (Table 5). Third, the product equation performed well in cross validation (LSF versus UMS data sets). The pool-cover and abundant rheophilic guilds were best predicted in cross validation, the pool-run guild was moderately successful, and the two rare (shallow-rheophilic and open-pool) guilds performed worst (Table 8). Analogously, Morin and Peters (1988) found the $R^2$ values to be similar for the original (''estimation'') and cross-validated data sets in polynomial equations to predict overall blackfly abundance in Quebec streams. In contrast, Shirvell (1989b) found much higher $R^2$ values for the verification data sets (50–96%) than for the validation data sets (7–30%) in the freshwater fish data sets that he reviewed.

We also examined the slope coefficients for the product equation ($B_p$) using unpooled-quadrat data (Table 5). As the values of $B_p$ were similar to those of analyses with pooled-quadrat data and few habitat categories, these slopes were robust. As shown in Table 9, these values were generally smaller for guilds of greater abundance and in analyses with fewer habitat categories. The latter result is intuitive because the use of fewer habitat categories meant greater averaging of data and thus lower maximum guild densities.

## *Formulation of Composite HSIs: Multiple-Regression Equations*

Further examination of the three multiple-regression equations (D4 to D6) yielded few consistently significant slope coefficients (Table 10). First, the individual SI of lowest value generally performed better than that of the highest value in the high-low equation (D5), suggesting that fish guild densities were influenced more by the worst than by the best habitat variable. Second, in the multiple-slope sum equation (D4), only four of the six guilds analyzed in both river segments showed consistently significant slope coefficients. These included (1) the fast-riffle guild, because it especially used shallow and fast waters; (2) the riffle-run guild, because it had an affinity for shallow microhabitats; (3) the open-pool guild, because it especially used finer substrata; and (4) the pool-cover guild, because it had an affinity for cover and slow velocities (Table 7; Figures 1, 2).

Third, the guild association equation (D6) generally verified the distinctiveness of the seven URR guilds (Table 10) that was evident in Table 7. The only consistently significant ($P \leq 0.001$) coefficient for rheophiles was that for the fast-riffle versus riffle-run guild densities. That is, these two guilds were generally both important in fast and slow riffles (Vadas and Orth 2000), even though the two guilds were most abundant in fast and moderate velocities, respectively (Figures 1, 2). Likewise, the shallow-rheophilic versus riffle-run coefficients were moderately significant ($P \leq 0.01$ to $P \leq 0.05$) in LSF; both guilds were abundant in slow riffles, although shallow rheophiles were also abundant in slower water (shallow pools). The two habitat-generalized guilds, namely the fast-generalist and pool-run guilds, showed moderate covariation; both were abundant in runs and pools, even though fast generalists were more abundant in riffles. The pool-run guild also showed high and

TABLE 9.—Maximum guild densities (fish per 100 m$^2$) for five physical-habitat variables and regression slopes for the product equation using pooled-quadrat data. Variables are defined in Table 2. Data were stratified by velocity variable ($V_a$, average velocity; $V_d$, demersal velocity), Roanoke River segment (lower South Fork [LSF] or upper main stem [UMS]), and number of mesohabitat categories (F, few; S, several). The highest suitability indices for a given row of data are underlined. See Tables 3, 4, and 7 for format and $R^2$ values, respectively.

| Guild | River segment | Meso-habitat cate-gories | Maximum guild density | | | | | Regression slopes | |
|---|---|---|---|---|---|---|---|---|---|
| | | | $C$ | $S$ | $D$ | $V_a$ | $V_d$ | $V_a$ | $V_d$ |
| Fast riffle | LSF | F | 9 | 11 | 15 | $\underline{17}$ | $\underline{22}$ | 1.39E−03 | 1.13E−03 |
| | | S | 9 | 14 | 15 | $\underline{19}$ | $\underline{22}$ | 1.41E−03 | 1.17E−03 |
| | UMS | F | 5 | 6 | 8 | $\underline{10}$ | $\underline{12}$ | 1.04E−02 | 8.76E−03 |
| | | S | 5 | 7 | 9 | $\underline{11}$ | $\underline{12}$ | 8.08E−03 | 7.43E−03 |
| Riffle–run | LSF | F | 46 | 66 | $\underline{99}$ | 50 | 68 | 1.01E−05 | 8.50E−06 |
| | | S | 60 | 88 | $\underline{186}$ | 51 | 79 | 7.65E−06 | 5.58E−06 |
| | UMS | F | 22 | 31 | $\underline{44}$ | 28 | 34 | 9.81E−05 | 8.86E−05 |
| | | S | 24 | 29 | $\underline{53}$ | 34 | 37 | 8.88E−05 | 8.48E−05 |
| Fast generalist | LSF | F | $\underline{18}$ | $\underline{18}$ | $\underline{18}$ | 17 | $\underline{18}$ | 3.24E−04 | 3.175E−04 |
| | | S | $\underline{24}$ | 18 | 21 | 18 | 20 | 3.035E−04 | 3.075E−04 |
| | UMS | F | 18 | 20 | $\underline{29}$ | 23 | 24 | 1.73E−04 | 1.63E−04 |
| | | S | 18 | 25 | $\underline{32}$ | 30 | 25 | 1.48E−04 | 1.465E−04 |
| Shallow rheophilic | LSF | F | 3 | 5 | $\underline{7}$ | 3 | 4 | 3.70E−02 | 3.22E−02 |
| | | S | 9 | 6 | $\underline{12}$ | 6 | 6 | 1.76E−02 | 1.75E−02 |
| Pool–run | LSF | F | 32 | 41 | $\underline{47}$ | 41 | 41 | 3.65E−05 | 3.56E−05 |
| | | S | 39 | $\underline{66}$ | 58 | 60 | 54 | 2.69E−05 | 2.50E−05 |
| | UMS | F | 18 | $\underline{20}$ | $\underline{20}$ | 19 | 17 | 3.26E−04 | 3.12E−04 |
| | | S | 21 | 20 | 22 | $\underline{24}$ | $\underline{26}$ | 3.36E−04 | 3.25E−04 |
| Open pool | LSF | F | 3 | $\underline{7}$ | 3 | $\underline{6}$ | 5 | 5.67E−02 | 6.69E−02 |
| | | S | 3 | $\underline{13}$ | 6 | 8 | $\underline{12}$ | 3.22E−02 | 2.32E−02 |
| | UMS | F | 2 | $\underline{5}$ | 2 | 2 | 2 | 1.57E−01 | 2.63E−01 |
| | | S | 2 | $\underline{6}$ | 3 | 3 | 4 | 2.03E−01 | 2.15E−01 |
| Pool cover | LSF | F | $\underline{13}$ | 11 | 8 | 12 | 11 | 2.20E−03 | 2.27E−03 |
| | | S | $\underline{21}$ | 15 | 12 | 18 | 18 | 1.30E−03 | 1.27E−03 |
| | UMS | F | $\underline{14}$ | 11 | 7 | 12 | 11 | 2.05E−03 | 2.19E−03 |
| | | S | $\underline{16}$ | 12 | 8 | 15 | $\underline{16}$ | 1.69E−03 | 1.59E−03 |
| Total number of underlines | | | 6 | 7 | $\underline{11}$ | 6 | 8 | | |

moderate covariation with the open-pool and pool-cover guilds, respectively; the three guilds were all abundant in pools, even though the pool-run guild was often found in faster water. In sum, these results and the species level analyses of Vadas and Orth (2000) highlight the distinctiveness of our seven guilds despite their partial overlap in certain habitat types.

### *Selection of the Best Composite HSI equation*

In sum, our pooled-quadrat results and the salmonid results of Lister (1988) suggest that aggregative HSI indices are similar in predictive power despite their differing assumptions. Hence, aggregation of SIs for the above physical variables may be satisfactorily accomplished via multiplication of the four individual SIs, as has traditionally been done to predict the density, relative abundance, or species diversity of zoobenthos (Orth and Maughan 1983; Gore 1989) and vertebrates in streams (Bovee 1986; Gore et al. 1992; Layher and Brunson 1992). That is, the product equation (D1) may provide as much predictive power for fish and macroinvertebrate densities as more complicated multiple-regression equations that account for animal-habitat interactions, despite the suggestions of some critics (e.g., Bain et al. 1982; Scott and Shirvell 1987). Although our pooling of SI data into guilds may have suppressed fish-habitat interactions at the species level, studies of salmonids such as brown trout *Salmo trutta* provide evidence for both independent and interdependent selection of habitat variables across streams (Gosse and Helm 1982; Shirvell 1986). Perhaps fish-habitat interactions are more common in watersheds with greater covariation among habitat variables than we found in the URR, although data from other streams suggest that depth, velocity, substratum-size, and cover variables lie on independent microhabitat axes (Vadas 1994).

Because the product equation is a simple, linear-regression model, it has two major advantages over multiple-regression equations, particularly those with polynomial and interaction terms. First, there

TABLE 10.—Minimum and maximum significance levels ($P$-values) for slope coefficients of multiple-regression equations (D4–D6) to predict the density of fish guilds from pooled-quadrat data. The abbreviation SI stands for suitability index; abbreviations $C$, $S$, $V$, and $D$ are explained in Table 2. All coefficients were positive except those indicated by the minus sign; ns = not significant; $P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.00$***. See Tables 3 and 8 for format and $R^2$ values, respectively.

| | High–low (D5) | | Multiple slope sum (D4) | | | |
|---|---|---|---|---|---|---|
| Guild | High | Low | $SI_C$ | $SI_S$ | $SI_V$ | $SI_D$ |
| Fast riffle (FR) | ns/* | ns/*** | ns/** | ns | *** | *** |
| Riffle–run (RR) | ns | *** | ns/*** | ns/* | ns/*** | *** |
| Fast generalist (FG) | ns | ns/*** | ns | ns | ns/** | ns/*** |
| Shallow rheophilic (SR) | ns | ** | ns | ns | ns | ** |
| Pool–run (PR) | ns | ns/*** | ns/* | ns | ns/* | ns/** |
| Open pool (OP) | ns/* | ns/*** | ns | ** | ns/* | ns |
| Pool cover (PC) | ns | ns/*** | *** | ns | **/*** | ns/* |

are fewer parameters to estimate. Second, multiple-regression equations are more likely to require site-specific, empirical estimation of slope coefficients because of multicollinearity problems (Draper and Smith 1981; Shirvell 1989b). Nevertheless, interaction assessment equations for fishes and other animals show evidence of quantitative consistency over time, albeit not for every habitat or biotic variable (Emlen et al. 1992). We agree with Gilchrist (1984) and Peters (1991) that the development of simple (e.g., regression) models with predictive power and testability across changing conditions should improve basic and applied ecological analyses; such cross-validated models are needed to determine the instream-flow needs of lotic organisms (Gore 1989). We nevertheless caution against the use of too few habitat variables for fishes, given that aquatic biota are unlikely to be limited by merely one or two factors, as implied by Leibig's law of the minimum (Lane and Levins 1977; Statzner et al. 1998) and the high-low equation (present study).

Finally, the higher predictive power for abundant rheophilic guilds than for abundant limnophilic guilds and (especially) rare guilds may reflect the greater importance of unmeasured environmental (biotic and abiotic) variables for the latter two groups (Freeman et al. 1997; but see Shirvell 1989b). For example, shallow rheophiles (the mountain redbelly dace *Phoxinus oreas* and the blacknose dace *Rhinichthys atratulus*) were found mostly in side channels (our personal observations, 1989–1991), perhaps because channel width is important to these headwater-oriented species in the URR drainage (Jenkins and Freeman 1972). Another likely explanation is that guild differences in spatial patchiness result from behavioral differences. Benthic rheophiles (e.g., several darters) often show greater site fidelity and territoriality than pelagic limnophiles (e.g., several minnows), which are usually more mobile, gregarious, and thus patchy and unpredictable via multispecific spawning (Jenkins and Freeman 1972; Vadas and Orth 1997) or schooling (Winn 1958; Moyle and Li 1979; Bart 1989; Vadas and Orth 1993) activities in streams. Species in rare guilds, including shallow rheophiles and the gregarious open-pool shiners, were even more patchy (clumped) than abundant limnophiles in the URR.

Clearly, further study is needed to corroborate clumping behavior as the cause of reductions in adjusted-$R^2$ values for HSI regressions. However, measurement of more environmental variables will not necessarily improve predictive ability if fish interdependently school back and forth among various good habitats. Indeed, the relatively sedentary and habitat-specialized behaviors of stream invertebrates may improve their HSI predictive power relative to that for mobile (nonriffle) fishes (Gore and Hamilton 1996; Gore et al. 1998), as well as make rheophilic invertebrates and fishes more sensitive to flow changes than limnophilic fishes (Gore 1989; Gore et al. 1992; Aadland 1993). Statzner et al. (1998) found that the product equation predicted insect abundance best when populations were abundant and patchy, which partially corroborates and partially contradicts our results.

### *Habitat Specialization and Important Habitat Variables*

The data in Table 9 also reveal that maximum densities were higher for the habitat variables that were most narrowly used by fish guilds (Tables 7, 10; Figures 1, 2). This is an intuitive result, because averaging of data into habitat categories would greatly attenuate maximum densities unless fish guilds were especially abundant in a minority of habitat conditions. First, the fast-riffle guild was

TABLE 10.—Extended.

| Guild | Guild association (D6) | | | | | | |
|---|---|---|---|---|---|---|---|
| | FR | RR | FG | SR | PR | OP | PC |
| Fast riffle (FR) | | *** | ns/* | ns | ns | ns | ns |
| Riffle–run (RR) | | | ns/*** | */** | ns | ns | ns |
| Fast generalist (FG) | | | | ns | */*** | ns/*(−) | ns |
| Shallow rheophilic (SR) | | | | | ns | ns | ns |
| Pool–run (PR) | | | | | | **/*** | */** |
| Open pool (OP) | | | | | | | ns |
| Pool cover (PC) | | | | | | | |

specialized for velocity, and to a lesser extent for depth and substratum size. Second, the riffle-run and shallow-rheophilic guilds were most specialized for depth, cover levels being least selected by the former guild. Third, the fast-generalist and pool-run guilds showed similar maximum densities for all habitat variables, which is evidence for their generalized use along several habitat axes, although fast generalists were most specialized for depth and the pool-run guild was least specialized for cover. Fourth, the open-pool guild was specialized for substratum size, and to a lesser extent for depth and velocity. Fifth, the pool-cover guild was most specialized for cover, with depth being the least-selected variable. Hence, the maximum-density method reaffirms the distinctiveness of the seven habitat use guilds and provides a simple, quantitative method for determining which habitat variables are critical for habitat selection. In contrast, the above analyses (Tables 7, 10) required more calculations and effort to interpret, and statistical significance was greatly affected by data distribution (violation of statistical assumptions), number of variables, and quadrat sample size.

Our results also suggest that depth was important more frequently than the other habitat variables for the URR fish assemblage (Table 9), as Shirvell (1989b) found in his meta-analysis of freshwater fish data. Likewise, Layher and Brunson (1992) found that the maximum standing crop of fishes (kg/ha) was much higher in relation to depth (650) than in relation to average water column velocity (275) or stream width (270) at a macrohabitat level in warmwater streams of Kansas. Hence, maximum-abundance data appear to be useful for establishing which habitat variables are most limiting and important for HSI modeling.

Maximum-abundance (density) data should be superior for building fish SI models—as compared with the traditional normalization of maximum SI values to unity (e.g., Bovee 1986)—because weighting variables by their importance can improve abundance (habitat availability) predictions over those provided by unweighted composite HSIs (Leclerc et al. 1995). Density data also provide a simpler method for weighting microhabitat variables than the weighted-product equation that Leclerc et al. (1995) used to aggregate SIs. Given that Leclerc et al. (1995) assigned the largest exponents to velocity (for Atlantic salmon fry) and to velocity and depth (for Atlantic salmon parr) and that data in the literature corroborate the relative importance of velocity for these rheophilic, immature fish (Bourgeois et al. 1996), we would expect maximum densities to be higher for hydraulic variables than for substratum size. Thevenet and Statzner (1999) similarly found that European stream fishes were best segregated by hydraulic and percent cover variables, although other bottom-topographic variables were important for some species. In summary, the URR guild data and species data from the literature suggest that hydraulic variables are more important than bottom-topographic factors for segregating fish species and guilds, which corroborates our previous species level analysis for the URR (Vadas and Orth 2000).

## Acknowledgments

We thank various undergraduate and graduate students for help with the fish habitat work and several landowners for providing access to study sites. The Virginia Water Resources Research Center funded the project, and the Canadian Department of the Environment, the U.S. National Marine Fisheries Service, and the Florida Marine Research Institute provided funding during manuscript revisions. P. L. Angermeier, E. F. Benfield,

C. A. Dolloff, and J. J. Ney critiqued early drafts of the initial manuscript, and later versions were improved by the comments of L. P. Aadland, K. D. Bovee, G. Henderson, and an anonymous reviewer. Finally, J. R. Ott provided the senior author inspiration to quantify fish cover use.

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