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Factors Influencing Behavior and Transferability of Habitat Models for a Benthic Stream Fish

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Abstract.—We examined the predictive power and transferability of habitat-based models by comparing associations of tangerine darter *Percina aurantiaca* and stream habitat at local and regional scales in North Fork Holston River (NFHR) and Little River, Virginia. Our models correctly predicted the presence or absence of tangerine darters in NFHR for 64% (local model) and 78% (regional model) of the sampled habitat-units (i.e., pools, runs, riffles). The distribution of tangerine darters apparently was influenced more by regional variables than local variables. Data from Little River and 37 historical records from Virginia were used to assess transferability of our models developed from NFHR data. In general, the models did not transfer well to Little River; all models predicted that either no (regional model) or few (local model) habitat-units in Little River would contain tangerine darter even though the species was observed in 83% of the habitat-units sampled. Conversely, the regional model correctly predicted presence of tangerine darters for 95% of the historical records. Principal components analysis showed extensive overlap in NFHR and Little River habitat which suggests that the two streams are ecologically similar. The suitability of Little River for tangerine darters was shown more clearly by principal components analysis than by our models. Because different limiting factors may apply in different systems, the elimination of potentially important ecological variables may compromise model transferability. A hierarchical approach to habitat modeling, with regard to variable retention, may improve transferability of habitat models.

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Models are widely used to predict occurrence, density, and habitat associations of aquatic species (Berry 1984; Fausch et al. 1988; Hobbs and Hanley 1990) and include effects of human impacts. Most habitat models for fish are based on the premise that physical characteristics influence fish occurrence, abundance, and production (Hubert and Rahel 1989), and numerous investigators have demonstrated these relationships by incorporating various physical and chemical variables into their models (Fausch et al. 1988). Relationships between habitat and fish populations, however, are complex and often poorly understood (Hubert and Rahel 1989), especially for nongame species. Thus, habitat models often lack precision for the system in which they were developed or are not transferable among systems (Layher et al. 1987).

Limitations to fish distribution and abundance may be viewed as a hierarchy. Ultimately, a species is limited by its physiological tolerance to physicochemical features such as dissolved oxygen, pH, and temperature. Within the range of its physiological tolerances and dispersal abilities, a species may be limited by availability of suitable physical habitat, which typically is described in terms of features like water depth, current velocity, substrate type, and cover. Physicochemical and structural features form habitat templates that constrain the types of life histories that can persist in a locality (Southwood 1977; Poff and Ward 1990; Townsend and Hildrew 1994). Finally, biotic features such as food, competitors, predators, and disease may further restrict distribution and abundance. All these limitations act concurrently to generate spatial variation in fish distributions and abundance, which can be modeled at a wide range of spatial scales. Accurate predictions of fish distribution and abundance may require complex models to account for variation both within and among spatial scales.

Ideally, species–habitat associations should be investigated across all pertinent scales (Morris 1987) because of the differential effects of regional- and local-scale patterns and their interactions on species distribution patterns. For example, Smogor et al. (1995) found that a single large-scale variable (distance to the ocean) predicted the distribution and abundance of the American eel *Anguilla rostrata* better than did local-scale variables (i.e., depth, current velocity, substrate, cover), whereas Ross et al. (1990) demonstrated both large- and local-scale features (stream size and microhabitat, respectively) influenced the distribution of the bayou darter *Etheostoma rubrum*. Models that account for variation at multiple spatiotemporal scales are likely to have greater predictive power than those focusing on a single scale.

Currently, no well-developed framework exists for predicting transferability of habitat models. Many habitat models are not transferable across spatiotemporal scales (Bowlby and Roff 1986; Angermeier 1987; Layher et al. 1987; Pajak and Neves 1987; Hubert and Rahel 1989), but some have transferred successfully (e.g. Belaud et al. 1989). Limited predictive ability and transferability may be caused in part by failure to include the "true" limiting habitat variables or by high spatiotemporal variability in these variables.

In this study we examined the predictive power and transferability of habitat-based models by comparing associations of tangerine darters *Percina aurantiaca* and stream habitat at two spatial scales. Tangerine darters were selected for study because they are relatively common and easily sighted by using underwater observation techniques (Greenburg 1991; Etnier and Starnes 1993; Jenkins and Burkhead 1994). Tangerine darters inhabit deep riffles, runs, and pools in relatively clear, moderate to large tributaries of the Tennessee River (Howell 1971; Greenburg 1991; Etnier and Starnes 1993; Jenkins and Burkhead 1994). These habitats are amenable to detailed underwater observations of habitat use and accurate estimates of abundance.

We first tested the null hypothesis that tangerine darters were uniformly distributed among stream habitats. Secondly, we tested the null hypothesis that habitat models developed in one stream were applicable in all streams where tangerine darters occur. We also examined patterns of model predictability and transferability by comparing logistic regression models, which retained only a few of the variables measured, with an ordination of habitats based on all measured variables.

Methods

Study streams.—North Fork Holston River (NFHR) and Little River, both in the upper Tennessee River system of southwestern Virginia, were selected for study because of high water clarity, the presence of substantial populations of tangerine darters (P. L. Angermeier, unpublished data), and similar water chemistry characteristics (Zipper et al. 1992).

North Fork Holston River is a sixth-order tributary of Holston River, Tennessee (Figure 1). It is a clear, slow moving, moderate gradient, warmwater stream characterized by alternating pool–

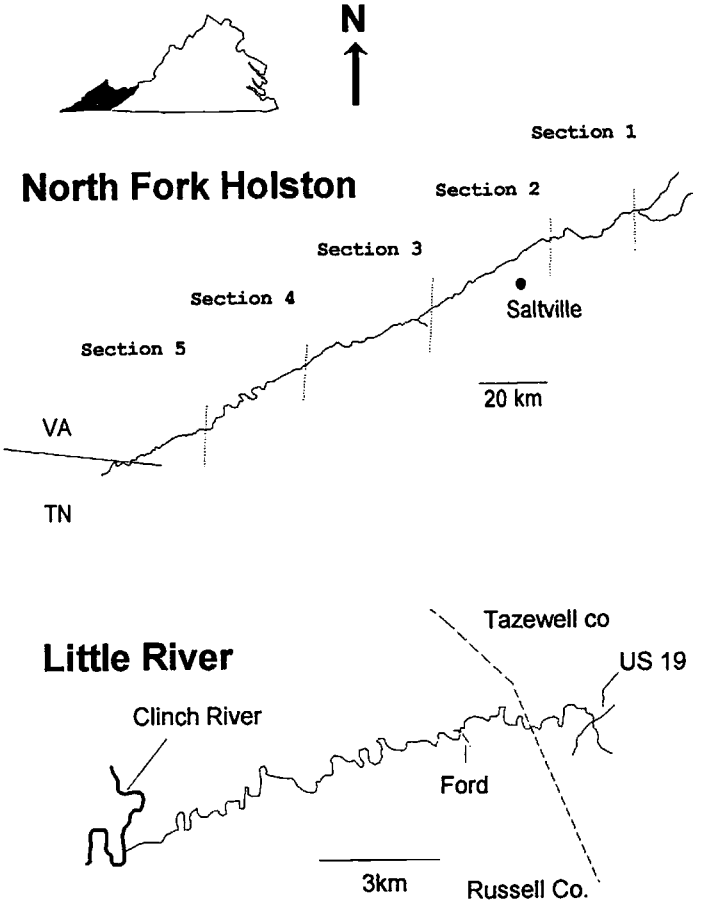

FIGURE 1.—North Fork Holston River (NFHR) and Little River in southwest Virginia. Broken lines on NFHR indicate endpoints of the five study reaches. Fish sampling in Little River started at the labeled ford and ended at the Clinch River confluence.

riffle morphology and a rocky substrate (Hill et al. 1975; Jenkins and Burkhead 1994). Land use is predominantly agriculture (livestock and row crops). A major source of industrial pollution to NFHR originated from Saltville, Virginia, during the late 1800s to the early 1970s (Jenkins and Burkhead 1994). Although the aquatic ecosystem below Saltville was changed dramatically by chemical pollution (Young-Morgan Associates 1990), substantial recovery has occurred in recent years (Hill et al. 1975; Feeman 1980; Jenkins and Burkhead 1994).

Little River is a moderate gradient, fourth-order tributary of Clinch River, Virginia (Jenkins and Burkhead 1994; Figure 1), characterized by an alternating pool–riffle morphology with gravel, cobble, and bedrock substrates. Only the lower 25 river kilometers support a warmwater fish fauna (Jenkins and Burkhead 1994). Little River flows through an agricultural valley without major industry (Jenkins and Burkhead 1994).

Habitat sampling.—We surveyed 180 contiguous river kilometers of NFHR from the Tennessee–Virginia border to the confluence of Lick Creek near Nebo, Virginia (stream width in the study ranged from 14 to 74 m during base flow), between June and September 1992 (Figure 1). This area encompasses the known range of tangerine darters in NFHR (Jenkins and Burkhead 1994). We divided the river into five sections of similar length for sampling and randomly selected the sampling order of the sections (Figure 1).

We surveyed the lower 16 river kilometers of Little River (stream width in the study ranged from 14 to 32 m during base flow) between May and July 1993 (Figure 1). We restricted sampling to this section because of low water clarity in the upper portion of the stream.

TABLE 1.—Ranges for categorical classes of continuous habitat variables as transformed into discrete variables (by using 50% or 25% quantiles). Habitat-unit measurements were used in logistic regression models and chi-square goodness-of-fit tests.

Habitat variable	Class 1	Class 2	Class 3	Class 4
Elevation (m)	≤408	409–463	464–536	>536
Length (m)	≤100	>100		
Width (m)	<21	22–31	32–44	>44
Depth (cm)	<25	26–50	51–75	>75
Distance to next similar unit (m)	≤100	>100		
Pool : riffle	≤0.82	0.83–1.64	1.65–3.33	>3.33

We used multistage, stratified sampling design and visual estimation techniques to estimate total surface area of selected habitat types (Hankin and Reeves 1988) and to determine the distribution of tangerine darters in NFHR and Little River. We based strata within reaches on naturally occurring habitat-units including pools, riffles, and runs.

A two-person crew classified and inventoried all habitat in NFHR and Little River study areas during periods of base flow. On the first of two trips down each river, one crew member identified each habitat-unit by type (pool, run, or riffle; Platts et al. 1983), visually classified the dominant and subdominant substrate by particle size (by using a modified Wentworth scale), and estimated wetted stream width. The other crew member estimated the depth-class (Table 1) of each habitat-unit by measuring depth (to the nearest 0.1 m) at about 3-m intervals while traveling downstream and across the channel in a zigzag pattern.

We measured the length of each habitat-unit with an optical range finder. We used these measurements and observations of landmarks to locate each habitat-unit on U.S. Geological Survey (USGS) 7.5′ topographic maps. We measured wetted stream widths (for calibration of habitat estimates) only in those units selected for fish sampling. We measured habitat and looked for tangerine darters in 26 pools, 47 riffles, and 38 runs in NFHR (10.8% of the habitat-units) and in 11 pools, 32 riffles, and 20 runs in Little River (35.2% of the habitat-units).

We made underwater observations during the second trip down each section of river to determine the distribution of tangerine darters within each selected habitat-unit. Two observers, equipped with face-masks and snorkels, entered the water at the downstream end of each selected habitat-unit and proceeded slowly upstream along a linear transect, continuously searching for tangerine darters. Transects were located in the areas of greatest flow in riffles and runs and about midway between the middle of the stream and the stream margin on each side for pools.

Sighting distance (distance from an observer to a visible Secchi disk) was measured at the beginning of each day of diver sampling and whenever visibility changed notably. Water clarity was considered suitable for underwater observations when sighting distance was greater than 1.5 m; visibility during sampling ranged from 1.5 to 4.1 m in NFHR and from 1.5 to 2.9 m in Little River.

Habitat variables.—Variables used in our analyses were (1) stream order, (2) stream elevation, (3) pool to riffle ratio (P:R), (4) habitat type, (5) dominant substrate, (6) subdominant substrate, (7) distance to the nearest habitat-unit of similar type, (8) habitat-unit length, (9) habitat-unit width, and (10) depth-class of the habitat-unit. We estimated mean elevation and stream order (Strahler 1957) of each sampled habitat-unit from USGS 7.5′ topographic maps (1:24,000 scale). We estimated P:R by dividing the surface area of pools by the surface area of runs and riffles within 500 m upstream and 500 m downstream of each habitat-unit sampled for fish. If an adjacent habitat-unit exceeded 500 m in length, a near-equal length of stream in the opposite direction was included in the calculation of P:R. For example, if the adjacent unit upstream of a sampled unit was a 800-m-long pool, then all of the downstream units within 800 m of the sample unit were included in the estimate of P:R.

Habitat models.—To test the first null hypothesis (tangerine darters were uniformly distributed) in the NFHR, we used multiple stepwise logistic regression (multivariate analysis) to generate three models to estimate the probability (chi-square probabilities < 0.05; SAS 1989) of tangerine darter occurrence (dependent variable) in NFHR habitat-units at two spatial scales (regional and local). We used presence–absence data because it is more robust to sampling biases than measures of densities (Green 1979).

The first model characterized regional conditions and included four independent variables: (1) stream width, (2) elevation, (3) stream order, and (4) P:R. The second model characterized local conditions and included six independent variables: (1) habitat type, (2) dominant substrate, (3) subdominant substrate, (4) habitat-unit length, (5) depth, and (6) distance to the next similar unit. The third model included all ten independent variables. Continuous habitat variables were transformed into discrete

variables by dividing the data into either two or four classes by using 50% or 25% quantiles, respectively (Table 1). We verified the three logistic regression models using univariate analyses (chi-square goodness-of-fit tests; $P < 0.05$) to examine associations between tangerine darter presence and individual variables used in logistic regression models.

Principal components analysis (PCA).—We used PCA (multivariate analysis; SAS 1989) to ordinate fish sampling units from both streams, based on all 10 habitat variables, to examine the effect of scale and variable reduction on model transferability. Because the ordinal data in our data set violated the assumption of multivariate normality required for statistical inference from PCA, we used this method only to illustrate similarity of sites across multiple ecological variables (Tabachnick and Fidell 1989; Johnson and Wichern 1992).

We performed PCA on two data sets: (1) NFHR sites and (2) NFHR and Little River sites combined. We compared the ordination of NFHR sites containing tangerine darters with the results of our logistic regression model (containing all ten habitat variables) and univariate analyses to assess the usefulness of PCA for identifying distribution patterns. If the ordination patterns of tangerine darters corresponded with the patterns of distribution in our previous analyses, then PCA would provide a reliable depiction of the similarity of habitat-units when both streams are ordinated together.

Model transferability.—To test our second null hypothesis (habitat models developed in one stream were applicable in all streams where tangerine darters occur), we used the three logistic regression models developed for NFHR to predict the presence and absence of tangerine darters in habitat-units of Little River. We verified model predictions with underwater observations.

We also compared the regional model predictions of tangerine darters presence with data from historical collection sites from the upper Tennessee drainage in Virginia (Burkhead and Jenkins 1991; Jenkins and Burkhead 1994). One site in the Powell River (sixth-order tributary of Clinch River), five sites in Copper Creek (fifth-order tributary of Clinch River), and 31 sites in Clinch River (seventh-order tributary of Tennessee River) were used to test the regional model. The degree of model transferability was assessed by the proportion of correct predictions.

Results

Logistic Regression

All three of our logistic regression models showed a nonuniform distribution of tangerine darters in NFHR. The regional model for NFHR indicated tangerine darters selected the higher order, lower elevation sections of the stream (Table 2). The logistic equation correctly predicted presence and absence of tangerine darters for 90 of 116 (78%) sampled habitat-units (critical probability = 0.5, SAS 1989; Table 3). The regional model correctly predicted presence (80% of observations) slightly more accurately than absence (76% of observations) of tangerine darters.

The local model indicated that tangerine darters selected habitat-units with a distance to the next similar habitat-unit of greater than 100 m with depths between 51 and 75 cm but avoided habitat-units with depths less than 25 cm (Table 2). The logistic equation predicted presence of tangerine darters correctly for 64% of the observations (Table 3). The local model correctly predicted darters presence (66% of observations) slightly more accurately than absence (64% of observations).

The regression model developed from all 10 habitat variables retained the same variables as the regional model but also indicated a positive association with streams greater than 43 m wide and a negative association with pebble as a subdominant substrate (Table 2). No significant variables in the local model emerged in this model, which correctly predicted absence (80% of observations)

TABLE 2.—Summary of stepwise logistic regression models to estimate probability of presence of tangerine darters in North Fork Holston River, Virginia. Parameter estimates are maximum-likelihood estimates, and significance of each variable is based on Wald chi-square. Significance of each model is based on a chi-square of the −2 log-likelihood statistic (SAS 1989); DU represents distance to next similar unit, and *S* represents subdominant substrate.

Variable	Parameter estimate	Chi-square	df	Probability
Regional model (χ^2 = 43.81, df = 2, P = 0.0001)				
Intercept	0.92	9.60	1	0.0020
Elevation > 463 m	−1.94	15.74	1	0.0001
4th order	−4.14	15.17	1	0.0001
Local model (χ^2 = 18.90, df = 3, P = 0.0003)				
Intercept	0.20	0.46	1	0.0498
Depth < 25 cm	−1.36	6.61	1	0.0102
Depth 51–75 cm	1.36	4.46	1	0.0347
DU < 100 m	−0.93	4.61	1	0.0317
Combined model (χ^2 = 56.88, df = 4, P = 0.0001)				
Intercept	1.11	7.86	1	0.0050
Width > 43 m	1.15	3.91	1	0.0479
Elevation > 463 m	−2.19	16.26	1	0.0001
4th order	−4.18	14.62	1	0.0001
Pebble (*S*)	−1.92	8.84	1	0.0030

TABLE 3.—Classification tables for the multiple logistic regression models in Table 2 to estimate probability of presence of tangerine darters in North Fork Holston River, Little River, and historical records. Classifications are based on critical values of 0.5 (SAS 1989).

Data set and observation	Number of habitat-units			
	Observed with fish	Predicted with fish		
		Present	Absent	Correct
North Fork Holston River				
Regional				
Present	50	40	10	
Absent	66	16	50	
Total	116	56	60	78%
Local				
Present	50	33	17	
Absent	66	24	42	
Total	116	67	69	64%
Combined				
Present	50	39	11	
Absent	66	13	53	
Total	116	52	64	79%
Little River				
Regional				
Present	52	0	52	
Absent	11	0	11	
Total	63	0	63	17%
Local				
Present	53	7	46	
Absent	10	2	8	
Total	63	9	54	24%
Combined				
Present	0	0	52	
Absent	63	0	11	
Total	63	0	63	17%
Historical records				
Regional				
Present	37	35	2	
Absent	0	0	0	
Total	37	35	2	95%

slightly more accurately than presence (78% of observations).

Chi-Square Analysis

Tangerine darters used the entire range of habitat available but preferred habitat-units in fifth- and sixth-order reaches at lower stream elevations that were longer than 100 m and wider than 32 m (Figure 2). These relationships corresponded with both the regional regression model and the regression model including all habitat variables and provided further evidence that tangerine darters avoided the smaller, upstream section of the NFHR study area.

Chi-square analyses did not support the regression models that contained local-scale variables. The relationships between tangerine darters and depth, observed in the local regression model, and between tangerine darters and pebble-subdominant substrate, observed in the regression model including all habitat variables, were not significant.

Principal Components Analysis

Visual representation of PCA closely corresponded with the results of the logistic regressions and univariate analyses at the regional scale and with the logistic regressions at the local scale. Tangerine darters were less common in lower order, higher elevation portions of NFHR (Figure 3A; Table 4). Habitat-units with the highest densities of tangerine darters (greater than 200/ha; K. N. Leftwich, unpublished data) were most common in moderate depths near the middle of NFHR, as indicated by stream order and elevation (Figure 3A).

Principal components analysis was partially successful at distinguishing NFHR sites from Little River sites but showed overlap (similarity) of numerous sites in both streams. The majority of sites occupied by tangerine darters in NFHR and Little River were similar (Figure 3B; Table 4).

Model Transferability

The logistic regression models developed from data collected in NFHR performed poorly when used to predict occurrence of tangerine darters in Little River (Table 3). The regional and local–regional (combined) models correctly predicted only the absence of tangerine darters and even then only in 17% of the 63 sampled units. These models predicted that no habitat-units would contain tangerine darters even though the species was observed in 83 percent of the units sampled. The local model performed slightly better than the regional model but predicted the correct condition for only 24% of the units sampled (Table 3). The regional model, however, correctly predicted presence of tangerine darters for 95% of the 37 historical records; it incorrectly predicted the absence of the darters for only two collections from the upper Clinch River (Table 3).

Discussion

Our results provided evidence to reject a uniform distribution of tangerine darter in NFHR. Our models demonstrated habitat selectivity by tangerine darter in NFHR at all spatial scales. Further, all analyses showed a relationship between tangerine darter distribution and stream size in NFHR.

Several analyses provided evidence that the distribution of the species is influenced more by regional than local patterns in NFHR. We found no significant relationships between presence of dart-

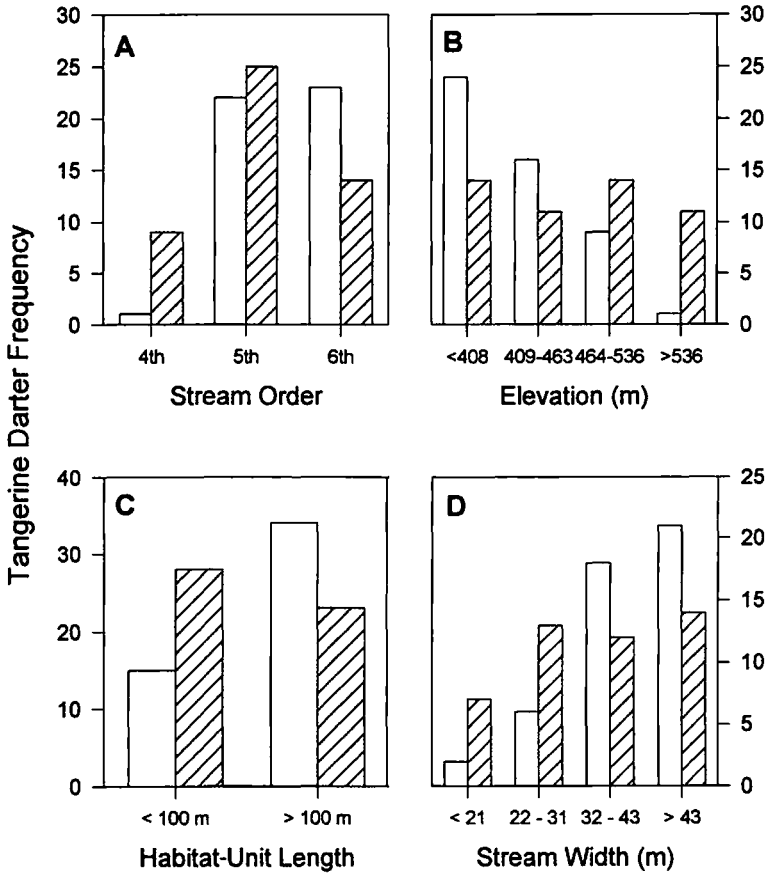

FIGURE 2.—Observed (open) and expected (hatched) frequencies from chi-square goodness-of-fit tests for tangerine darter observations in North Fork Holston River: (**A**) stream order ($P < 0.005$; df = 2), (**B**) elevation ($P < 0.005$; df = 3), (**C**) habitat-unit length ($P < 0.025$; df = 1), and (**D**) stream width ($P < 0.005$; df = 3).

ers in the chi-square analyses of local factors, and regional variables dominated the regional–local (combined) model. The PCA also supported the influence of regional conditions in NFHR. These results suggest that within suitable stream reaches, tangerine darters are not restricted to a narrow range of local habitat conditions in NFHR.

This finding may explain the success of the regional models in predicting the presence of tangerine darters in historical collection sites. With the exception of two sites in upper Clinch River (for which the regional model incorrectly predicted the species as absent), the historical collections were taken from streams in the same size and elevation range as those identified by the regional model for NFHR.

Our results provided evidence to reject the hypothesis of model transferability. Neither the regional model nor the local model transferred well to Little River or historical sites in the upper Clinch River. These results are similar to those from studies of the transferability of habitat suitability index models (see Bowlby and Roff 1986; Layher et al. 1987; Hubert and Rahel 1989; Groshens and Orth 1994). The wide but unpredictable distribution of tangerine darters in Little River suggests that the environmental factor(s) that limits the species distribution either was not included (or retained) in these models or differed from that in NFHR.

The role of limiting factors in population ecology has been a subject of debate for most of this century. Allen (1926) suggested that many variables may contribute to observed patterns, even if the evidence points to one factor. The relative importance of each variable as a limiting factor may vary considerably among systems. A particular variable will only appear as a limiting factor when its values cluster near the limits of the range of tolerance of the target species. As such, limiting

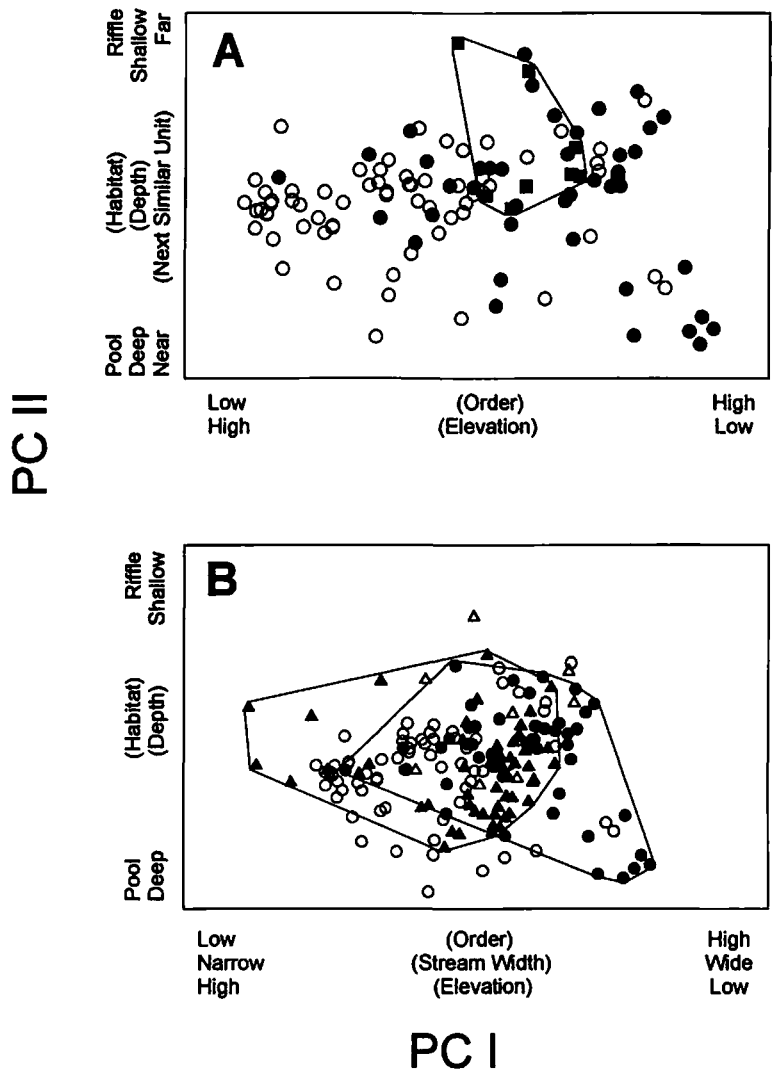

FIGURE 3.—Plots of habitat-units in principal components (PC) space based on 10 habitat variables. (A) Plot of habitat-units in North Fork Holston River (NFHR). Open circles represent sites lacking tangerine darters, solid circles represent sites containing tangerine darters, and solid squares, encompassed by a polygon, represent sites with tangerine darter densities greater than 200/ha. (B) Plot of habitat-units in NFHR and Little River. Circles and triangles represent habitat-units in NFHR and Little River, respectively, where tangerine darters were present (closed) and absent (open). Polygons encompass sites occupied by tangerine darters in NFHR and Little River.

factors may be ranked in different orders among systems. Thus, reduced or simple models may not transfer well because key variables that explain species distributions in some systems but not others have been removed.

Because habitat models are typically constructed by eliminating some variables, some resolution in habitat associations may be lost. Logistic regression models developed for tangerine darters incorrectly predicted the species to be either absent or nearly absent from Little River. The PCA plot of habitat-units from both rivers (Figure 3), however, showed that many habitat-units in Little River are similar to those occupied by tangerine darters in NFHR. The ordination of habitat-units, based on all variables, more clearly showed the suitability of Little River habitat for tangerine darters than did the logistic regression models, which were based on fewer variables.

A hierarchical approach to modeling habitat as-

TABLE 4.—Results of principal component (PC) ordination of sampled habitat-units from North Fork Holston River (NFHR; N = 116) and Little River (N = 63) based on 10 habitat variables. Eigenvectors associated with each variable for the first three PCs from the NFHR are shown with eigenvalues of respective correlation matrices and proportions of variance explained. Eigenvectors with absolute values less than 0.3 are represented by dashes.

Variable or statistic	PC I	PC II	PC III
North Fork Holston River			
Order	0.492	–	–
Elevation	−0.529	–	–
Riffle–pool	–	–	0.640
Mean stream width	0.467	–	–
Habitat-unit type	–	0.550	–
Distance to like unit	–	0.432	–
Habitat-unit length	–	−0.320	–
Depth	0.347	−0.428	–
Dominant substrate	–	–	−0.562
Subdominant substrate	–	–	0.374
Eigenvalue	3.039	2.088	1.225
Proportion of variance	0.304	0.209	0.123
NFHR–Little River combined			
Order	0.500	–	–
Elevation	−0.528	–	–
Riffle–pool	–	–	0.401
Mean stream width	0.476	–	–
Habitat-unit type	–	0.574	–
Distance to like unit	–	0.346	–
Habitat-unit length	–	−0.350	–
Depth	–	−0.519	–
Dominant substrate	–	–	−0.675
Subdominant substrate	–	–	0.514
Eigenvalue	3.247	1.972	1.201
Proportion of variance	0.325	0.197	0.120

sociations may improve model transferability. A full-model approach may be useful in determining the overall similarity of the systems being studied. Once ecological similarity has been established, reduced models may be used to identify specific habitat needs or limitations of a species at various spatial scales. For example, the glochidia of the Cumberland monkeyface *Quadrula intermedia*, a freshwater mussel, only survive on the gills of two host-fish species in the genus *Erimystax*. Further, this species has been found only in moderate to large streams, in swift-water habitats, and over silt-free rocky substrates (Neves 1991). *Quadrula intermedia* is thus a highly specialized species with very specific habitat requirements. A transferable model for *Q. intermedia* might consist of three levels: (1) presence of host species, (2) stream size, and (3) local current velocity and substrate. A hierarchical approach, however, may only apply where the modeler's objectives include developing models with broad applicability.

In summary, we reject the hypothesis that tangerine darters were uniformly distributed in NFHR. Our models demonstrated habitat selectivity by tangerine darters in NFHR at all spatial scales, and habitat selectivity at the regional scale was verified by chi-square analyses.

We also reject the hypothesis that habitat models developed for tangerine darters in the NFHR were applicable to all streams in southwest Virginia. Our logistic models incorrectly predicted the distribution of tangerine darters in Little River and upper Clinch River. Although tangerine darter distribution in NFHR and most of the historic sampling sites might have been explained by regional variables, tangerine darter occurrence was not predicted in Little River or the upper Clinch River sites.

Finally, PCA more clearly illustrated the suitability of Little River as habitat for tangerine darters than did our models. The loss of resolution, caused by the elimination of potentially important ecological variables, may compromise the transferability of habitat models. A hierarchical approach to habitat modeling, with regard to variable retention, may improve transferability of habitat models across spatial scales and across stream systems.

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