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Transferability of Habitat Suitability Criteria for Fishes in Warmwater Streams

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Abstract.—We developed habitat suitability criteria and tested their transferability for nine fishes inhabiting unregulated Piedmont and Coastal Plain streams in Alabama. Criteria for optimal habitat were defined as those ranges of depth, velocity, substrate type, and cover type for which a species' suitability index (proportional abundance divided by proportional habitat availability, scaled from 0 to 1) equalled or exceeded 0.4. We evaluated the transferability of criteria between study sites by testing the null hypothesis that species occurrence in a sample was independent of whether or not the sample was taken in optimal habitat. We also tested criteria transference to a large, flow-regulated river sampled during low-flow periods. Depth, velocity, and most substrate criteria developed for the bronze darter *Percina palmaris* successfully transferred between unregulated streams and to the flow-regulated river samples. All criteria developed for a pair of closely related, allopatric darter species, the newly described lipstick darter *Etheostoma chuckwachatte* and the greenbreast darter *E. jordani*, transferred successfully when applied between species (in the unregulated sites) and to the regulated river samples. In contrast, criteria for the Alabama shiner *Cyprinella callistia* failed nearly all tests of transferability. Criteria for the speckled darter *E. stigmaeum*, the blackbanded darter *P. nigrofasciata*, an undescribed *Percina* species, and a pair of related, allopatric *Cyprinella* species transferred inconsistently. The species with good criteria transference had high suitability indices for the shallow depths, fast current velocities, and coarse substrates characteristic of riffle species. We suggest that microhabitat criteria for riffle fishes are more likely to provide a transferable measure of habitat quality than criteria for fishes that, although restricted to fluvial habitats, commonly occupy a variety of pool and riffle habitats.

Determining instream flow requirements for sustaining populations of fishes poses a major challenge to agencies responsible for managing stream resources. One widely used method for analyzing the effects of changes in flow regime on stream populations, the physical habitat simulation (PHABSIM) component of the instream flow incremental methodology (IFIM; Bovee 1982), combines hydraulic simulations with habitat criteria to estimate flow-related changes in the amount and quality of habitat available to target species. Habitat criteria specify microhabitat requirements, usually in terms of water depth, current velocity, and substrate type, for species of interest (Bovee 1986). Clearly, the validity of a PHABSIM analysis partly depends on how accurately the habitat criteria describe habitat requirements of the target organisms.

Habitat suitability criteria have been developed for a variety of fishes in a diverse array of stream systems, and these criteria often agree with more general, qualitative descriptions of fish habitat use. However, a number of studies have demonstrated differences among criteria developed for different populations of a particular species (Bozek and Rahel 1992; Groshens and Orth 1993) or between generic (i.e., based on literature and field data from a variety of localities) and site-specific criteria (Shirvell 1989; Waite and Barnhart 1992; Groshens and Orth 1993). Habitat suitability criteria may also vary for fish inhabiting different macrohabitats (e.g., riffles, runs, or pools) in the same stream (Modde and Hardy 1992; Vondracek and Longanecker 1993) and between feeding and nonfeeding periods (Kwak et al. 1992). As Modde and Hardy (1992) point out, many of these differences are intuitive and result from variation in habitat availability, food availability, and possibly competition or predation (Moyle and Baltz 1985; Orth 1987).

Considerations of the numerous factors influencing habitat use suggest the use of site-specific habitat criteria in instream flow analyses whenever possible (Moyle and Baltz 1985). However, on-site development of habitat criteria in streams with modified flow-regimes or degraded habitat may not

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TABLE 1.—Locations and descriptions of study sites used for development of habitat suitability criteria. All sites were located in Alabama.

Site (abbreviation)	Location	Description
Piedmont 1 (P1)	Enitachopco Creek, Tallapoosa County, about 5.6 air km WNW of Goldville (Tallapoosa River system)	Alternating riffle, run, and pool habitat; boulder, cobble, gravel, and sand substrates; riverweed *Podostemum ceratophyllum* common; site length = 413 m; average width = 21 m
Piedmont 2 (P2)	Hatchet Creek, Coosa County, about 3.4 air km NW of Goodwater (Coosa River system)	Riffle–run habitat in upstream and downstream portions, separated by a 170-m-long pool; boulder, cobble, gravel, and sand substrates; riverweed common in riffles; site length = 264 m; average width = 18 m
Coastal Plain 1 (C1)	West Fork Choctawhatchee River, Dale County, about 6.1 air km W of Echo (Choctawhatchee River system)	Predominantly sand- and gravel-bottomed pool habitat, with one 90 m-long riffle over rock and compacted clay; abundant woody debris (tree trunks, branches) in channel; site length = 334 m; average width = 16 m
Coastal Plain 2 (C2)	Whitewater Creek, Coffee County, about 4.2 air km WNW of Victoria (Pea River system)	Sand-bottomed pool in upper half of site, with abundant woody debris; riffle–run habitat over cobble and compacted clay in lower half, site length = 296 m; average width = 14 m

reflect the actual habitat preferences or requirements for maintaining strong populations, particularly if target species are confined to low-quality habitat (Tyus 1992). For example, mobile fishes may persist in degraded reaches only as a result of immigration from other, higher-quality portions of the system. In this case, habitat criteria developed in streams supporting strong populations could better describe a species' habitat requirements than criteria developed on-site, but only if those criteria accurately reflect habitat quality independently of site-specific habitat features.

The objective of this study was to measure the transferability of habitat criteria for fishes between unregulated stream systems and to a larger, flow-regulated river in order to evaluate the potential for developing broadly transferable criteria for warmwater stream fishes. We followed Thomas and Bovee (1993) in defining transferability as the ability of criteria to correctly specify optimal habitat, such that fish are more likely to occupy optimal habitat than habitat classified as nonoptimal. We developed criteria from samples taken during a single season to minimize effects of changes in behavior or habitat availability on patterns of habitat use and then tested criteria transferability between streams of similar size and habitat structure and to samples collected during low-flow periods in a flow-regulated river. The failure of criteria to transfer even between similar streams in a single season would indicate that site-specific differences may in fact confound development of general habitat suitability criteria for those species. Conversely, good transference across streams would indicate that those criteria reflect habitat requirements and may be useful for habitat assessments in a wider range of streams.

Methods

We developed habitat suitability criteria (HSC) using data collected in two Piedmont and two Coastal Plain streams in central and south Alabama (Table 1) during July, August, and September 1992. Flow in all streams was unregulated, and there were forested riparian zones at the study sites. We sampled fish with prepositioned area electroshockers. We used a bottom unit (two 1.5-m-long electrodes separated by 0.75 m) in depths less than about 0.6 m and a suspended unit (four 1.5-m-long electrodes, 0.75 m apart) in depths of 0.6 to 1.2 m (see Fisher and Brown [1993] for a complete description of electrode design). Deploying the units involved securing an overhead cable and wiring harness across the width of the stream at a selected location and positioning the electrode units at predetermined locations across the cable. Electrode units were connected one at a time to the wiring harness and a Smith-Root model 3.5 GPP pulsator that was powered by a 120-V AC generator. The pulsator and generator were located in a floating barge positioned near the streambank. We left the electrodes in place and undisturbed for at least 10 min before applying power to the first unit. Two persons held a seine or nets downstream from the electrodes while power was on (20 s total) and collected electroshocked fish from the area. Workers then thoroughly searched the electroshocked area and collected stunned fish from the stream bottom. Collected fish were anes-

and sandbar habitats. We recorded the dominant substrate type and measured depth and current velocity at five points (each corner and middle) at the location of each fish sample; cover characteristics were not recorded. We averaged the depth and velocity measurements and used the most frequently recorded substrate type to characterize habitat for each sample. Collected fishes were preserved and returned to a laboratory for identification.

To test for transferability of suitability criteria, we generally followed the procedure outlined by Thomas and Bovee (1993). This method requires designating appropriate ranges of habitat variables as optimal for the study species. For example, Thomas and Bovee (1993) defined the central 50% of frequency distributions of occupied depths and velocities as optimal habitat for rainbow trout *Oncorhynchus mykiss*. Groshens and Orth (1993) defined habitat ranges for which suitability indices (SI) equalled or exceeded 0.7 (on a scale of 0 to 1) as optimal for smallmouth bass *Micropterus dolomieu*. We designated the range of each habitat variable for which SI equalled or exceeded 0.4 as optimal habitat for each species (or length-class). The choice of 0.4 as a defining point generally resulted in criteria for optimal habitat that included ranges of variables with calculated preference greater than 1 (i.e., proportional use greater than proportional availability) and excluded categories with preference less than 1. For example, 91% of depth and velocity intervals with preference scores greater than 1 also had SIs of 0.4 or higher (scores combined across all species and sites). Conversely, 8% of depth and velocity intervals with preference scores less than 1 had SIs of 0.4 or higher.

Using criteria for optimal habitat developed in a given stream, we cross-classified samples from a target site as either optimal or nonoptimal with respect to that variable and either occupied (i.e., containing the target species or length class) or unoccupied. A chi-square test of independence (Conover 1971) applied to this 2 × 2 matrix tested the null hypothesis that species occurrence in a target-site sample was independent of whether the sample was located in optimal or nonoptimal conditions. This test assumed that both optimal and nonoptimal conditions were available and sampled.

Our analysis differed from procedures used by Thomas and Bovee (1993) in three respects. Thomas and Bovee required that criteria for both "optimal" and "suitable" habitat (defined as the habitat variable intervals containing the central 50% and 95%, respectively, of occupied locations) pass tests of transferability in order for the HSC to be considered transferable. We used a more conservative procedure by only testing transferability of criteria for optimal habitat. We hypothesized that if HSC based on microhabitat measurements provided accurate descriptions of a species' habitat requirements, then the narrower range of frequently occupied microhabitats (used to define optimal habitat) should consistently predict where fish occurred within different sites, whereas occurrence in a broader range of microhabitats should be more strongly influenced by relative habitat availability and population density. Testing transference of optimal habitat criteria may more directly address the ability of microhabitat measurements to describe habitat requirements independently of site-specific conditions. We also separately tested criteria for each habitat variable, whereas Thomas and Bovee tested variables in combination and defined a location as optimal habitat only if values for depth, velocity, and cover were all optimum. Testing habitat variables singly allows a consideration of whether some variables consistently transfer and can thus provide a better measure of habitat suitability than others. Finally, Thomas and Bovee used a one-sided chi-square test, which we could not use because we did not have independent data sets describing habitat availability or fish habitat use. Instead, we had one sample of size N from a site, with each element classified as either optimal or not and as occupied by a given species or not, to which we could apply a two-sided chi-square test of independence.

We tested the transference of criteria for up to four habitat variables for each species and set a probability level of 0.1 for rejecting the null hypothesis. Because tests of individual variables were not independent, we applied the sequential Bonferroni technique (Rice 1989) to adjust probability levels so that the type I error rate was held to 0.1 for each species in each test of criteria transference.

Results

The 1992 samples yielded relatively diverse collections of fishes, from 22 to 33 species per site, of which five or six species occurred in at least 25 samples in one or both Piedmont sites (Table 2). The Coastal Plain sites had only a single species, the blackbanded darter, that occurred in 25 or more samples. Most species were infrequently captured; only four of the species that occurred in fewer than 25 samples (and were thus excluded from further analysis) were represented by more than 20 individuals at any site.

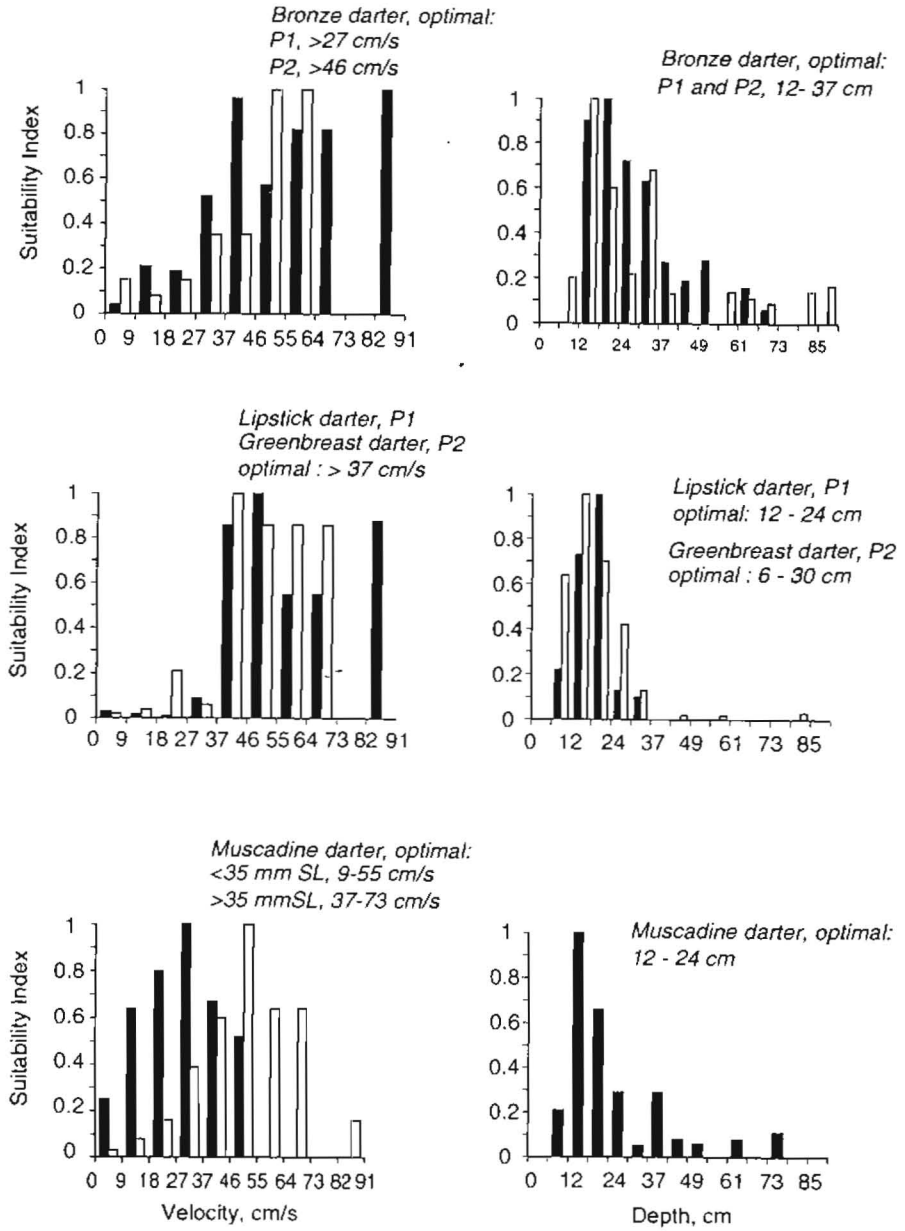

FIGURE 1.—Depth and velocity suitability indices for the bronze darter, lipstick darter, and greenbreast darter at study sites P1 (dark bars) and P2 (open bars). Velocity indices for the muscadine darter are for small (dark) and large (open) individuals in P1. Ranges of depth and velocity designated as optimal for testing criteria transference are indicated above each plot.

shiners, speckled darters (Figure 2), and black-banded darters (Figure 3) displayed less consistent responses to most variables, with high SIs across wider ranges of depth, velocity, and a variety of substrate and cover types (Table 3).

The ranges of each habitat variable designated as optimal for testing criteria transferability are shown in Figures 1–3 and Table 3. In three cases, we ignored high SIs that were disparate from remaining values and that resulted from a few (2–4) fish occurring in depth or velocity intervals with low proportional availability (Figures 2, 3). Oth-

TABLE 3.—Substrate and cover types defined as optimal (suitability index ≥ 0.4) in development of habitat suitability criteria.

Species and site	Substrate	Cover
Bronze darter, P1	Sand, gravel, pebble, cobble	Velocity shelter, riverweed
Bronze darter, P2	Cobble, boulder	Riverweed
Lipstick darter, P1	Pebble, cobble	Velocity shelter, riverweed
Greenbreast darter, P2	Cobble, boulder	Riverweed
Muscadine darter, P1	Pebble	Velocity shelter, riverweed
Tallapoosa shiner, P1	Silt, pebble, cobble	Riverweed, snags, debris
Tricolor shiner, P2	Gravel, pebble, boulder, bedrock	Velocity shelter, riverweed
Speckled darter, P1	Silt, sand,[a] pebble, boulder,[a] bedrock[b]	Velocity shelter, snags, debris
Speckled darter, P2	Sand, gravel	No cover, snags, riverweed
Alabama shiner, P1	Silt,[a] pebble,[a] cobbler,[b] boulder	Velocity shelter,[b] snags, riverweed,[a] debris
Alabama shiner, P2	Gravel, pebble, bedrock	Riverweed
Blackbanded darter, C1	Sand, bedrock	Velocity shelter, snags
Blackbanded darter, C2	Debris, silt, sand, gravel, cobble, boulder, bedrock	No cover, velocity shelter, snags, debris

[a] Individuals ≤35 mm SL only
[b] Individuals >35 mm SL only.

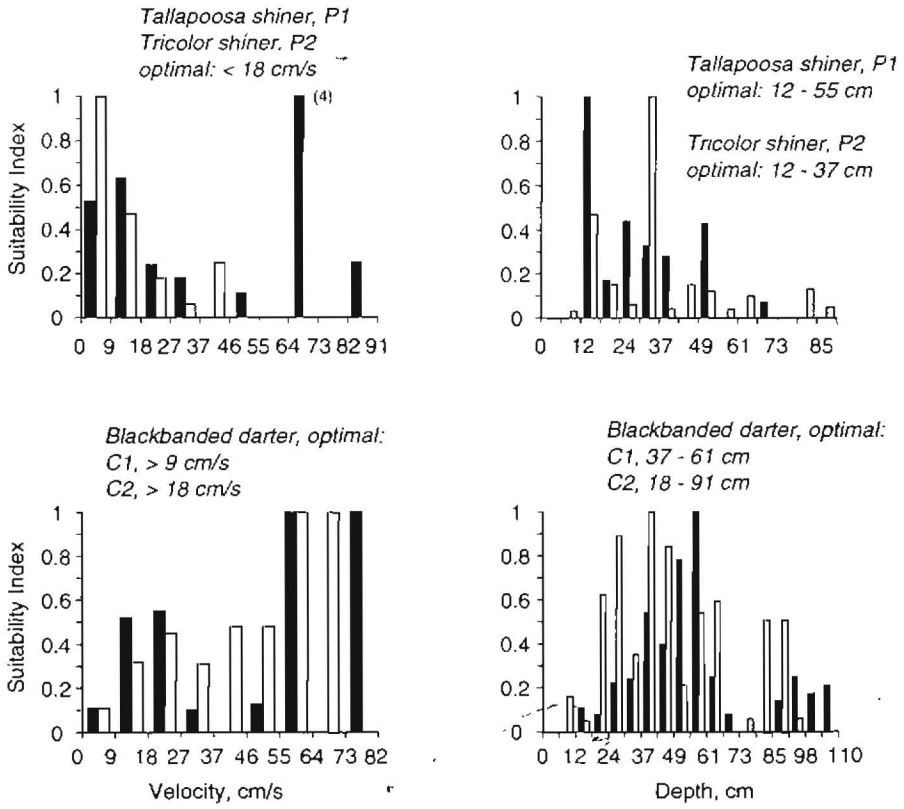

FIGURE 3.—Depth and velocity suitability indices for the Tallapoosa shiner (dark bars) and the tricolor shiner (open bars) and for the blackbanded darter in study sites C1 (dark) and C2 (open). Ranges of depth and velocity designated as optimal for testing criteria transference are indicated above each plot. Values in parentheses beside histogram bars show the number of individuals captured in intervals that were excluded from optimal criteria ranges.

that variables interact to determine habitat suitability. Lacking prior knowledge of which habitat variables, individually or in combinations, most strongly influence microhabitat use, testing transference of variables one at a time may allow detection of habitat factors that consistently correlate with species occurrence and those that do not. This could help ensure that univariate HSC used in PHABSIM analyses incorporate variables that are relevant to actual habitat suitability for a given species.

Nearly all criteria developed for two darter species that were abundant in swift, shallow areas transferred well between similar unregulated streams (with the greenbreast darter as a surrogate for the lipstick darter at one site) and to regulated river samples collected during low-flow intervals. Depth criteria for small Alabama shiners also transferred between similar-sized streams and to the regulated river samples. Criteria that specified cobble and boulder as preferred substrates in the mid-sized streams proved predictive of species occurrence in the large river samples. Velocity criteria for the blackbanded darter transferred between Coastal Plain streams but did not predict occurrence in large river samples. In addition, most habitat suitability criteria developed for the Alabama shiner did not transfer, even between similar mid-sized streams. Criteria for another pair of minnows, the Tallapoosa and tricolor shiners, transferred inconsistently between similar streams, possibly indicating that these closely related taxa in fact differed in habitat requirements. Criteria for the speckled darter also transferred inconsistently between similar streams, although velocity criteria did transfer to the large river samples.

Examination of tests where criteria failed to transfer suggested that in some cases (i.e., about one-third of the failed tests between mid-sized streams) there was an insufficient range of microhabitat conditions available for the contingency tests to show significant dependence between species occurrence and habitat optimality. These were cases in which large percentages of both the occupied and unoccupied samples occurred in optimal conditions. This does not imply that criteria would have discriminated occupied from unoccupied samples if fish had experienced a broader habitat gradient, but only emphasizes the necessity of developing and testing criteria under conditions where both optimal and nonoptimal conditions are available (Bovee 1986). In addition, total sample sizes in the unregulated streams were considerably lower than the values of at least 55 occupied samples and 200 unoccupied samples recommended by Thomas and Bovee (1993) for testing criteria transferability. We do not know to what extent transference failure resulted from type II error, and certainly more extensive testing is warranted for criteria that appeared to describe microhabitat use across streams fairly well but failed transference tests. However, the lack of transference of most criteria for the Alabama shiner strongly contrasts with the nearly total success of criteria transference, even to the regulated river sites, for the bronze darter and lipstick darter. One implication is that stream fishes differ in the extent to which microhabitat measurements adequately describe habitat quality.

A goal of defining binary (i.e., optimal versus nonoptimal) suitability criteria is to distinguish those habitat conditions with the greatest probability of sustaining populations of the target species. Suitability criteria calculated from a species' abundance in particular microhabitats, relative to overall availability of those microhabitats, rest on the assumption that animals preferentially occupy areas that best support survival, growth, or reproduction. If this is the case, then suitability criteria based on species occurrence across microhabitat gradients should reflect those habitat conditions most critical for preserving populations. Successful criteria transference would indicate consistent preference for particular microhabitat conditions, supporting the assumption that those conditions reflect habitat quality for the species. Conversely, criteria may fail to transfer because (1) the preferred conditions are unavailable; (2) target species abundance or sample sizes are insufficient to observe preference (Thomas and Bovee 1993); (3) other factors, such as competition or predation (Orth 1987), prevent animals from using preferred habitats; or (4) criteria do not describe preferred or critical microhabitats.

Species that occupy a range of stream macrohabitats may also occur over a broad range of microhabitat conditions, which may or may not strongly relate to overall habitat suitability. For example, smallmouth bass and many stream cyprinids (Leonard and Orth 1988; Lobb and Orth 1991; Aadland 1993) as well as salmonids (Modde and Hardy 1992) often use high-velocity riffle and run habitats as well as low-velocity eddy and pool habitats. Foraging profitability likely depends on flow patterns and prey density, density of other foragers, and predation risk. Microhabitat criteria based on depth and velocity measurements at or near the point of capture are likely to be broad for

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