ARTICLE

Scale-Dependent Seasonal Pool Habitat Use by Sympatric Wild Brook Trout and Brown Trout Populations

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Abstract

Sympatric populations of native Brook Trout *Salvelinus fontinalis* and naturalized Brown Trout *Salmo trutta* exist throughout the eastern USA. An understanding of habitat use by sympatric populations is of importance for fisheries management agencies because of the close association between habitat and population dynamics. Moreover, habitat use by stream-dwelling salmonids may be further complicated by several factors, including the potential for fish to display scale-dependent habitat use. Discrete-choice models were used to (1) evaluate fall and early winter daytime habitat use by sympatric Brook Trout and Brown Trout populations based on available residual pool habitat within a stream network and (2) assess the sensitivity of inferred habitat use to changes in the spatial scale of the assumed available habitat. Trout exhibited an overall preference for pool habitats over nonpool habitats; however, the use of pools was nonlinear over time. Brook Trout displayed a greater preference for deep residual pool habitats than for shallow pool and nonpool habitats, whereas Brown Trout selected for all pool habitat categories similarly. Habitat use by both species was found to be scale dependent. At the smallest spatial scale (50 m), habitat use was primarily related to the time of year and fish weight. However, at larger spatial scales (250 and 450 m), habitat use varied over time according to the study stream in which a fish was located. Scale-dependent relationships in seasonal habitat use by Brook Trout and Brown Trout highlight the importance of considering scale when attempting to make inferences about habitat use; fisheries managers may want to consider identifying the appropriate spatial scale when devising actions to restore and protect Brook Trout populations and their habitats.

The protection and enhancement of stream habitats constitute a common goal for fisheries management agencies, largely due to the close association between habitat and fish population dynamics (Rosenfeld and Hatfield 2006). In fact, a lack of suitable habitat may influence populations through effects on individual fitness (e.g., survival, growth, and reproductive success) and may limit abundance if certain habitats that are needed to complete critical life stages are limited or lacking (Rosenfeld and Hatfield 2006). Habitat characteristics that are necessary for maintaining healthy salmonid populations often include adequate streamflow, low-velocity and deepwater refuge, foraging sites, overhead cover, and spawning gravels (Fausch et al. 1988).

Although the relationship between habitat use and fish population dynamics has been studied for some species (e.g., Young 1996; Muhlfeld and Marotz 2005), uncertainties in seasonal habitat use still exist for eastern Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta*, especially in stream systems where these species are sympatric. The Brook Trout is a keystone coldwater fish species (PADCNR 2010) that is ecologically and economically important throughout its native range. Unfortunately, Brook Trout populations do not persist in the same abundances as they did historically (EBTJV 2011). The majority of population declines have been attributed to the

degradation of streams' physical and chemical (i.e., water quality) habitat characteristics, primarily due to anthropogenic alterations of the landscape (Malmqvist and Rundle 2002; Stranko et al. 2008). In addition, interaction with nonnative species has also been identified as a threat to native Brook Trout populations. Throughout much of the Brook Trout's native range in the eastern USA, the threat is posed by interactions with naturalized Brown Trout populations (EBJTV 2011).

A better understanding of temporal and spatial variation in habitat use by Brook Trout and Brown Trout would benefit resource management agencies' efforts to protect, enhance, and manage existing Brook Trout populations. Information on trout habitat use could assist future management, conservation, and restoration efforts in several ways (Neely et al. 2010). For example, it may aid in the identification of specific habitats that are necessary for completing certain life history requirements (Saiget et al. 2007). Knowledge of Brook Trout habitat use can also assist management agencies in assessing the effects of physical and chemical habitat disturbances on population dynamics, ultimately aiding evaluations of the costs and benefits involved in conserving, restoring, and managing the population (Jones and Tonn 2004).

Habitat selection by Brook Trout has been studied in some areas within the species' native range (Baker et al. 1996; Baird and Krueger 2003; Petty et al. 2005, 2012; Mollenhauer et al. 2013), and several studies have revealed the spatial and temporal dynamics of habitat selection by Brown Trout under differing flow regimes (Ayllón et al. 2010, 2014). However, few studies have focused on quantifying habitat use by both Brook Trout and Brown Trout within the same time period and in the same geographic location (Baird et al. 2006). Furthermore, the majority of studies examining habitat use by Brook Trout and Brown Trout have been restricted to a single study reach over a relatively short time frame. Although the importance of general habitat characteristics has been demonstrated for stream-dwelling salmonid populations, drawing inferences about stream fish habitat use is complicated by several factors, including the potential for fish to display scale-dependent habitat use (Baxter and Hauer 2000; Feist et al. 2003). In other words, our inferences might be affected by the presumed scale at which (1) habitat use is controlled and (2) habitat is "available" to an individual fish at any given time. The objectives of the present study were to (1) evaluate fall and early winter daytime habitat use by Brook Trout and Brown Trout based on the available residual pool habitat within a stream network; and (2) assess the sensitivity of inferred habitat use to changes in the spatial scale at which habitat is assumed to be available for an individual fish at a given point in time. We focused on the use of pool habitats due to their importance for salmonids (e.g., Solazzi et al. 2000; Hakala and Hartman 2004) and because we could effectively quantify this habitat characteristic throughout the entire study area.

METHODS

Study site.—Study streams were located in the Hunts Run watershed, north-central Pennsylvania (Figure 1). The Hunts Run watershed, located primarily in Cameron County, has a 79.2-km^2 drainage area and is primarily forested with deciduous hardwood and evergreen tree species. The study streams included the Hunts Run main stem and four of its tributaries: McKinnon Branch, McNuff Branch, Rock Run, and Whitehead Run (Figure 1). Brook Trout density in these streams ranged from 1.1 to 9.7 fish/100 m^2, and Brown Trout density ranged from 0.7 to 15.8 fish/100 m^2 (Davis et al. 2015).

Fish sampling.—Brook Trout (55 individuals) and Brown Trout (45 individuals; hereafter, the two species are collectively referred to as "trout") were sampled between September 13 and 20, 2012, and received surgically implanted Lotek NanoTag Series digitally coded transmitters (NTC-3-2; weight = 1.1 g; active between 0600 and 1800 hours; Lotek Wireless, Inc., Newmarket, Ontario). A crew worked upstream to capture trout by using pulsed-DC electrofishing; the numbers of trout collected were 13 Brook Trout and 17 Brown Trout in Hunts Run; 10 Brook Trout and 10 Brown Trout in McKinnon Branch; 8 Brook Trout and 12 Brown Trout in McNuff Branch; 14 Brook Trout and 6 Brown Trout in Whitehead Run; and 10 Brook Trout in Rock Run. Brook Trout weighed 45–417 g (102 ± 60 g [mean ± SD]) and had FLs of 162–345 mm (214 ± 32 mm). Brown Trout weighed 46–829 g (166 ± 158 g) and had FLs of 161–430 mm (246 ± 49 mm). All trout were presumed to be sexually mature and age 1 or older; however, sex could not be confidently determined for all fish. Fish were sampled throughout each stream reach in order to obtain an even distribution in stream distance between individuals, and the fish were released into the stream near the point of capture.

Quantifying available pool habitat.—To assess whether the use of specific habitats was disproportionate to their availability, we quantified available habitat for the entire stream network. Thalweg profiles were used to quantify the available pool habitat (Mossop and Bradford 2006; Mollenhauer et al. 2013) by measuring stream channel morphology and creating a longitudinal profile of physical stream habitat. Thalweg profiles provide a repeatable, quantitative, continuous measure of stream pool habitat over an entire stream or stream segment, and they allow measurements to be independent of streamflow and discharge. The thalweg profiles were then used to identify and quantify residual pool habitat (Mossop and Bradford 2006). Residual pools constituted the primary metric examined in this study because of pools' known importance for salmonid populations, including Brook Trout and Brown Trout (Cunjak and Power 1986; Clapp et al. 1990; Nickelson et al. 1992; Solazzi et al. 2000; Hakala and Hartman 2004).

To identify residual pools, the streambed elevation along the deepest point (i.e., thalweg) of the stream was measured longitudinally. Any changes in streambed elevation or depth
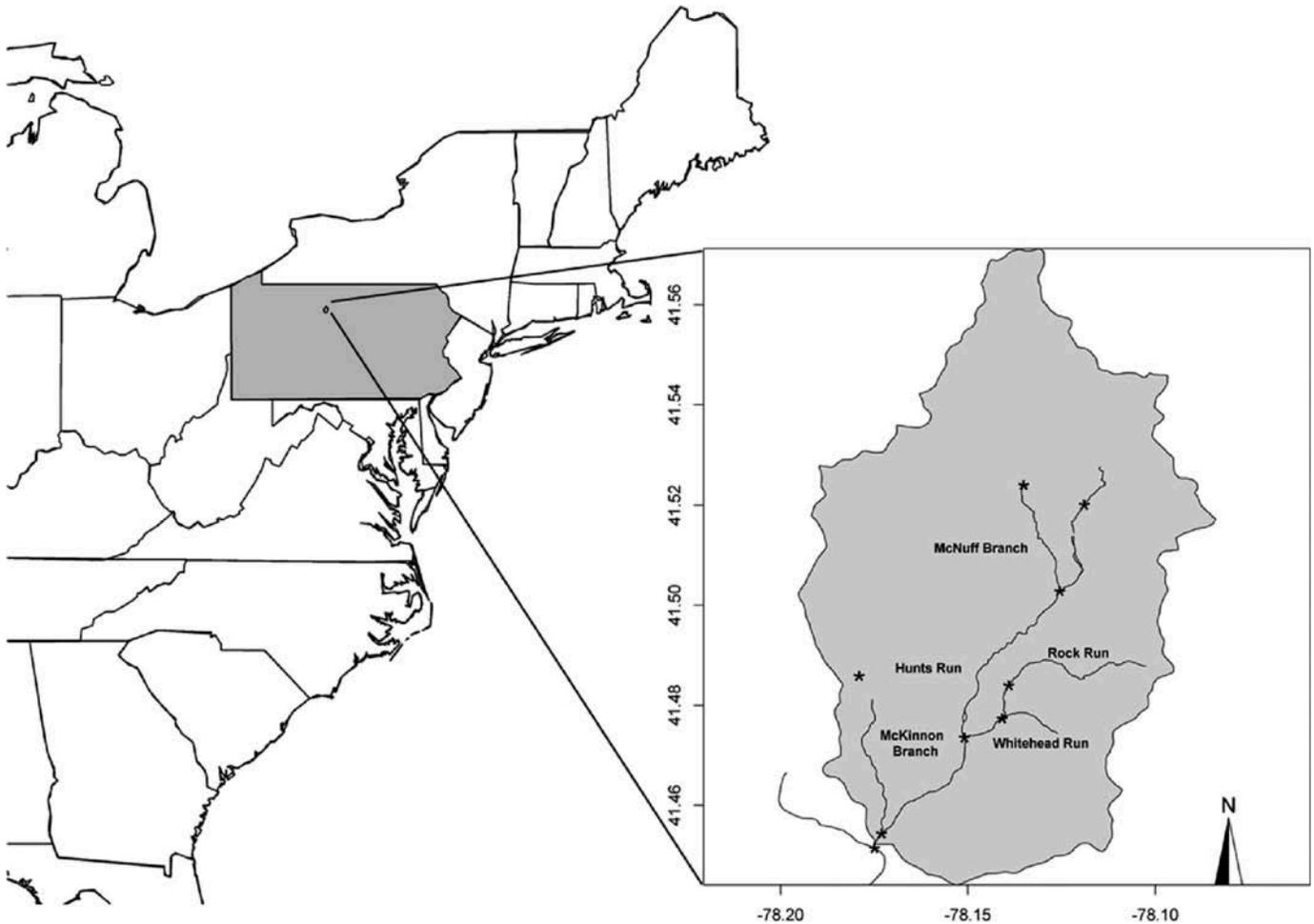
FIGURE 1. Map of study streams located in the Hunts Run watershed of north-central Pennsylvania. Asterisks indicate upper and lower limits of thalweg profiles on each stream (note that McKinnon Branch extends beyond the line shown on the map to the asterisk).

(≥0.1 m) were classified as representing residual pools (Lisle 1987). This streambed elevation criterion was used to avoid overclassification of pool habitat, caused by designating minor streambed irregularities as pools (Mossop and Bradford 2006). Standard surveying techniques were used to survey thalweg profiles of study streams (Harrelson et al. 1994). Using a laser level, stadia rod, and measuring tape, a two-person crew worked upstream and recorded the elevation and distance along the thalweg every 5 m or at a break (reduction in elevation) in the slope of the streambed. This break indicated the "boundary" of a potential residual pool (downstream riffle crest). The greatest reduction in elevation from the boundary (i.e., the deepest point) was recorded. In addition, the upstream point that corresponded as closely as possible to the boundary's elevation was recorded. Based on these measurements, the maximum residual pool depth and the residual pool length were calculated. Using a Trimble GeoXH 6000 Centimeter Edition GPS unit (Trimble Navigation, Inc., Sunnyvale, California), location was recorded every 50 m of

longitudinal stream distance or when the stream channel made an abrupt change in direction.

Longitudinal profiles were created for each of the five study streams: surveyed reach lengths were 11.7 km in Hunts Run, 4.1 km in McKinnon Branch, 3.0 km in McNuff Branch, 1.4 km in Whitehead Run, and 847 m in Rock Run, resulting in a total of approximately 21 km of stream reach surveyed (Figure 1). Due to a large vertical waterfall on Rock Run (~2.5 m in height), only a small reach of that stream (847 m) was surveyed. Surveying did not occur above the barrier because the probability of trout moving upstream beyond that point was low. Digital maps of the streams were created by assigning a latitude and longitude to each elevation measurement of the thalweg profiles based on the linear distance between the logged GPS points.

Habitat use.—Individual fish telemetry locations from 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013, in the Hunts Run watershed were used to determine the type of

habitat used (i.e., the shallow pool, deep pool, or nonpool habitat occupied) by each individual fish. Radio-tracking was performed by two crews of two persons each; fish were typically located one to two times per week during September through December and were located biweekly thereafter due to an observed reduction in fish movement. Either visual identification or signal strength was used to identify the location of a given fish. Based on the locations of expulsed or predator-consumed transmitters as well as trials during which crew members hid transmitters, the signal strength error was estimated to be within 1 m^2 of the actual fish's location. Once a fish was located, its GPS location was logged using a Trimble GeoXH 6000 Centimeter Edition GPS unit. Using Trimble Terrasync field software coupled with Trimble Pathfinder office software, locations were carrier post-processed for a GPS accuracy within 1 cm.

Statistical analysis.—Discrete-choice models with random effects were used to model habitat use by trout. As described by Kneib et al. (2011), a discrete-choice model is a multinomial logit model that assumes the occurrence of k habitat types. Observations are collected at different time points (not necessarily equal) on n animals. The probability that habitat type r is chosen at time t by fish j is denoted by $\pi_{jt}^{(r)}$ and is related to fish-specific and habitat-specific covariates:

$$\pi_{jt}^{(r)} \propto A_{jt}^{(r)} \exp\left[n_{jt}^{(r)}\right], \qquad (1)$$

where $\propto$ denotes proportionality up to a multiplicative constant; and $n_{jt}^{(r)}$ is an additive predictor of habitat type r at time t for fish j. The additive predictor is of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + x_{jt}'\gamma^{(r)} + \sum_{i=1}^{p1} f_i^{(r)}(u_{jti}). \qquad (2)$$

The components of models (1) and (2) are as follows: $A_{jt}^{(r)}$ is the availability of habitat type r at time t for fish j; $A_{jt}^{(r)}$ is referred to as an offset and is a known constant that is proportional to the habitat fraction of the available space. The inclusion of availability allows for the determination of whether habitat use is selective and/or disproportionate to availability. The symbol $\beta^{(r)}$ represents parameters that indicate the overall habitat preference by trout once the possible covariate effects and availability are accounted for. Positive values for parameter estimates would indicate that use of the habitat type is proportionately greater than its availability in the choice set. Individual fish-specific random effects are denoted as $b_j^{(r)}$ and are used to account for correlations between observations on a given fish. The random effects of different fish are assumed to be independent and identically distributed as $b_j^{(r)} \sim \text{Normal}(0, \tau_r^2)$, with category-specific variance τ_r^2 (Kneib et al. 2011). Linear effects of time and fish-specific covariates x_{jt} correspond to the

parameters $\gamma^{(r)}$. Nonparametric effects of time and continuous fish-specific covariates u_{jti} correspond to $f_i^{(r)}(u_{jti})$, where the nonparametric functions are habitat category specific and where the covariates are globally defined (see Kneib et al. 2011 for details). The nonparametric effects were modeled by using a basis functions approach, and overfitting was avoided by the introduction of a roughness penalty on the regression coefficients (Kneib et al. 2011).

Available habitat choice set.—Available habitat in discrete-choice models is quantified based on the percentage of each habitat category within each choice set. The residual pool habitat data from the thalweg profiles were used to quantify available habitat; habitat categories were then created based on residual pool depths, and the percentage of each available residual pool habitat category was calculated based on the lengths of each residual pool habitat. Due to the lack of any a priori hypotheses for defining residual pool depth categories, the 75th quartile of residual pool depth was used as a cutoff to define two pool categories: deep and shallow. Although the definition of pool categories based on measured stream-specific distributions of residual pools was statistically based rather than ecologically based, we felt this to be the most appropriate approach given that the published literature is deficient in determined thresholds for defining pool habitats relative to trout. Furthermore, given the importance of pool habitat for stream-dwelling salmonids (Clapp et al. 1990; Jakober et al. 1998), our categorization should still have ecological relevance. Residual pools with depth values greater than or equal to the 75th quartile value were classified as deep pools, whereas shallow pools were defined as any residual pool with a depth value less than the 75th quartile. This classification yielded three habitat categories (shallow pool, deep pool, and nonpool). Because the streams differed in their thalweg profiles, stream-specific habitat categories were created. Habitat was also quantified for each fish location (i.e., habitat used by trout) according to the three habitat categories.

Choice sets.—For each fish location, the amount of habitat (i.e., the proportions of shallow pool, deep pool, and nonpool habitats) considered available to that individual fish at that point in time was calculated. Thus, the proportion of available habitat from each category changed each time a fish moved. To examine whether our inferences were sensitive to assumptions about how much stream habitat was "available" to a fish at any point in time, we evaluated three spatial scales (stream lengths) based on the median daily movement of fish observed throughout the study period (Davis et al. 2015): 50, 250, and 450 m. The amount of stream considered available was based on the stream length derived from the longitudinal profiles. Available habitat was calculated by using equal distances upstream and downstream of each fish location; thus, at the 50-m scale, the habitat from 25 m upstream to 25 m downstream of the fish's location was

considered available to the fish at that point in time. Likewise, at the 250-m scale, the habitat from 125 m upstream to 125 m downstream of the fish's location was considered available; at the 450-m scale, the habitat from 225 m upstream to 225 m downstream of the fish location was considered available.

Candidate models.—Ten a priori candidate models were fitted to explain habitat selection by trout at the three spatial scales (50, 250, and 450 m) that were used to quantify available habitat. For all models, the reference habitat category was nonpool habitat because we predicted that trout would primarily select for the two residual pool categories over the nonpool category. Habitat use model (HM) 1 was an unconditional model with the hypothesis that habitat selection by Brook Trout and Brown Trout was based only on the residual pool depth of available habitat. The additive predictor for HM1 was of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)}. \tag{3}$$

Habitat use model 2 addressed the hypothesis that habitat selection at a certain time of year was based on residual pool depth, given the prediction that habitat selection would differ according to the time of year since trout may select for different habitats during the spawning season. The spawning period for Brook Trout extends from mid-September through November, whereas Brown Trout spawn in October–December. Time was represented as the study day (the first day of tracking was day 1, the second day was day 2, up to day 163) and was standardized ($\mathrm{time}_i - \overline{\mathrm{time}_i} / \mathrm{SD}[\mathrm{time}]$) to improve convergence. Time was a continuous covariate and a nonparametric effect in the model. The additive predictor for HM2 was of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + \sum_{i=1}^{p1} f_i^{(r)}(u_{jti}). \tag{4}$$

For HM3, the hypothesis was that habitat selection was based on residual pool depth and species association (trout species). Species was expressed as a fish-specific covariate in the model, with Brook Trout set as the reference cell. The additive predictor was of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + x_{jt}' \gamma^{(r)}. \tag{5}$$

Habitat use model 4 addressed the hypothesis that habitat selection at a certain time of the year was influenced by residual pool depth and species association. Time and species were included in the model as previously described. The additive predictor for HM4 was of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + x_{jt}' \gamma^{(r)} + \sum_{i=1}^{p1} f_i^{(r)}(u_{jti}). \tag{6}$$

Because habitat preference may be size dependent, the hypothesis for HM5 was that habitat selection at a certain

time of the year was influenced by residual pool depth and individual fish weight. Fish weight was chosen as an overall metric of fish condition and was $\log_e$ transformed for all models. Time and $\log_e$(fish weight) were expressed as continuous covariates and nonparametric effects in the model. The HM5 predictor was of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + \sum_{i=1}^{p1} f_i^{(r)}(u_{jti}). \tag{7}$$

The hypothesis for HM6 was that habitat selection at a certain time of year was influenced by residual pool depth, individual fish weight, and stream association (i.e., the stream in which a trout was located). Stream was expressed as a categorical fish-specific covariate with Hunts Run, McKinnon Branch, and McNuff Branch as categories; McNuff Branch was set as the reference stream. We initially attempted to include trout that were located in Whitehead Run and Rock Run; however, model convergence issues prevented the inclusion of those fish in the analyses. The predictor for HM6 was of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + \sum_{i=1}^{p1} f_i^{(r)}(u_{jti}) + x_{jt}' \gamma^{(r)}. \tag{8}$$

Habitat use model 7 evaluated the interaction between time of year and stream association to examine whether fish in different study streams selected for differing habitats at certain times of the year. The interaction of these two covariates was expressed as a nonparametric effect in the model. The predictor was of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + \sum_{p1}^{i=1} f_i^{(r)}(u_{jti}) \cdot x_{jt}' \gamma^{(r)}. \tag{9}$$

Habitat use model 8 involved the hypothesis that habitat selection at a certain time of the year was influenced by residual pool depth, individual fish weight, and stream association. The HM8 predictor was of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + x_{jt}' \gamma^{(r)} + \sum_{i=1}^{p1} f_i^{(r)}(u_{jti}). \tag{10}$$

Habitat use model 9 represented the hypothesis that habitat selection was influenced by residual pool depth, fish weight, species association, and the time of year × stream association interaction. The predictor for HM9 was of the form

$$\begin{aligned} n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + x_{jt}' \gamma^{(r)} \\ + \sum_{i=1}^{p1} f_i^{(r)}(u_{jti}) + \sum_{i=1}^{p1} f_i^{(r)}(u_{jti}) \cdot x_{jt}' \gamma^{(r)}. \end{aligned} \tag{11}$$

Due to species-specific differences in spawning season timing, Brook Trout and Brown Trout may also select for different habitats at different times of year. Therefore, HM10 evaluated the time of year × species interaction. This model included residual pool depth, time of year, and species as

covariates. The time of year × species interaction was expressed as a nonparametric effect in the model. The predictor for HM10 was of the form

$$n_{jt}^{(r)} = \beta^{(r)} + b_j^{(r)} + \sum\nolimits_{i=1}^{p1} f_i^{(r)}(u_{jti}) \cdot x_{jt}' \gamma^{(r)}. \quad (12)$$

Model comparison.—All models were fitted using BayesX version 2.1 software. Models were ranked within each of the three spatial scales by using Akaike's information criterion (AIC). Because there are inherent difficulties in counting the number of parameters estimated when fitting models with random effects, we used the equivalent degrees of freedom as a measure of the effective number of parameters in each model. The AIC was calculated using the effective degrees of freedom as a measure of model complexity. Models within the same spatial scale were ranked based on the AIC difference (ΔAIC), which for model i was calculated as $\Delta AIC_i = AIC_i - AIC_{min}$, where AIC_{min} represents the lowest AIC value (best-performing model) observed among all candidate models within that spatial scale. Akaike weights (w_i) were then calculated for all models j as $w_i = \exp(0.5 \cdot \Delta AIC_i) \sum_{j=1}^{J} \exp(0.5 \cdot \Delta AIC_j)$.

RESULTS

In total, 31 Brook Trout and 40 Brown Trout were included in the habitat use models for Hunts Run (12 Brook Trout and 23 Brown Trout), McKinnon Branch (10 Brook Trout and 9 Brown Trout), and McNuff Branch (10 Brook Trout and 8 Brown Trout). Available habitat sets were calculated for 1,498 individual fish telemetry locations. Of those fish locations, 694 were recorded in Hunts Run, 360 were obtained in McKinnon Branch, and 444 were recorded in McNuff Branch. The shallow residual pool category was defined as 0.10–0.38 m for Hunts Run, 0.10–0.34 m for McKinnon Branch, and 0.10–0.32 m for McNuff Branch. The deep residual pool category was defined as 0.39–1.40 m for Hunts Run, 0.35–1.10 m for McKinnon Branch, and 0.33–1.50 m for McNuff Branch. Habitat category percentages (calculated based on the total length of each residual pool habitat category across the entire reach of each stream) were 25% shallow pool, 22% deep pool, and 53% nonpool for Hunts Run; 23% shallow pool, 19% deep pool, and 58% nonpool for McKinnon Branch; and 18% shallow pool, 14% deep pool, and 68% nonpool for McNuff Branch. Unconditional models (HM1) fitted at each spatial scale (50, 250, and 450 m) indicated that there was an overall selection for residual pool habitats in preference to nonpool habitats; however, HM1 received little support when describing habitat use by both species overall (Tables 1, 2). Furthermore, individual fish varied in their selection for shallow pools and deep pools across each of the three spatial scales; variability was greatest for the use of shallow pools at the 50-m scale (Table 1; Figure 2).

Model rankings differed among the three spatial scales. At the 50-m scale, HM6 ($w_i = 0.27$) and HM8 ($w_i = 0.17$) received some support (Table 2), but the top-ranked model at

TABLE 1. Unconditional discrete-choice models describing trout habitat use at three spatial scales (50, 250, and 450 m) for 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013, in the Hunts Run watershed, Pennsylvania. Nonpool habitat served as the reference habitat category to which shallow pools and deep pools were compared. Each species' estimated preference for each pool habitat category ($\hat{\beta}$; defined by maximum residual pool depth) is provided along with the estimated SD and 95% confidence interval (CI). The symbol $\hat{\tau}_r^2$ represents an individual-specific random effect describing variability among individuals in the selection of each pool habitat category.

Spatial scale or habitat category	$\hat{\beta}$	SD	95% CI	$\hat{\tau}_r^2$
50-m scale				
Shallow pool	2.91	0.284	2.35–3.47	1.82
Deep pool	3.91	0.261	3.39–4.42	1.58
250-m scale				
Shallow pool	1.53	0.182	1.17–1.88	1.10
Deep pool	2.80	0.177	2.45–3.14	1.15
450-m scale				
Shallow pool	0.82	0.170	0.48–1.15	0.93
Deep pool	2.18	0.182	1.81–2.53	1.35

that spatial scale was HM5 ($w_i = 0.54$), which included the nonparametric effects of time and $\log_e$(fish weight). In contrast, at both the 250- and 450-m spatial scales, the top-ranked model was HM9 ($w_i = 0.65$ and 0.61, respectively); HM8 ($w_i = 0.20$) received some support at the 250-m scale, and HM7 ($w_i = 0.40$) received some support at the 450-m scale. Habitat use model 9 included the species effect, the nonparametric effect of $\log_e$(fish weight), and the time of year × stream association interaction (Table 2). Variability among individual fish was consistent between HM1 and the top-ranked models at each spatial scale. Variability in the use of shallow and deep residual pools remained low overall among individuals even when covariates were included in the models.

Both Brook Trout and Brown Trout exhibited greater selection for residual pool habitats than for nonpool habitat under the top-ranked model at the 50-m scale, HM5 (Table 3). Because the effects of time and $\log_e$(fish weight) were modeled nonparametrically, we do not provide parameter estimates but instead present them visually in Figures 3 and 4. The use of both residual pool habitats varied minimally over time. However, there was a slight decrease in the selection of deep residual pool habitat during mid-November (Figure 3). Although fish weight was a nonparametric effect in the model, there was an overall positive linear relationship between $\log_e$(fish weight) and the selection of both shallow and deep residual pool habitats. Thus, heavier Brook Trout and Brown Trout displayed greater selection for shallow and deep residual pool habitats over nonpool habitat (Figure 4).

The top-ranked model at the 250- and 450-m spatial scales, HM9, indicated an overall preference for residual pool habitats over nonpool habitat. However, Brook Trout and Brown Trout

TABLE 2. Candidate discrete-choice models with individual fish-specific random effects describing habitat selection by 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013, in the Hunts Run watershed at the 50-, 250-, and 450-m spatial scales (HM = habitat use model). Covariates incorporated into each model are listed (d = residual pool depth; t = time [standardized]; w = $\log_e$ transformed fish weight; st = stream in which a fish was located; sp = trout species; + = additive covariates; × = interactions). Also shown are the equivalent degrees of freedom (df); –2 times the log likelihood (–2log$L$); Akaike's information criterion (AIC); the AIC difference between the given model and the best-performing model (ΔAIC$_i$); and Akaike weight (w_i). Models are listed in order from lowest to highest AIC value.

Spatial scale or model	Covariates	df	–2log$L$	AIC	ΔAIC$_i$	w_i
50-m scale						
HM5	$d + t + w$	63.22	735.22	861.68	0.00	0.54
HM6	$d + t + w + st$	64.96	733.11	863.04	1.36	0.27
HM8	$d + w + st$	66.28	731.41	863.98	2.30	0.17
HM2	$d + t$	65.87	738.18	869.93	8.25	0.01
HM4	$d + t + sp$	66.42	737.13	869.97	8.29	0.01
HM7	$d + (t \times st)$	69.71	732.76	872.19	10.51	0.00
HM10	$d + (t \times sp)$	68.78	738.44	873.37	11.69	0.00
HM9	$d + w + sp + (t \times st)$	70.97	731.42	873.37	11.69	0.00
HM1	d	62.86	772.84	898.57	36.89	0.00
HM3	$d + sp$	63.55	772.03	899.93	37.47	0.00
250-m scale						
HM9	$d + w + sp + (t \times st)$	98.88	1,737.56	1,935.34	0.00	0.64
HM8	$d + w + st$	97.78	1,742.11	1,937.67	2.33	0.20
HM6	$d + t + w + st$	92.52	1,753.81	1,938.86	3.52	0.11
HM7	$d + (t \times st)$	91.37	1,758.48	1,941.22	5.88	0.03
HM4	$d + t + sp$	88.26	1,767.75	1,944.27	8.93	0.01
HM5	$d + t + w$	87.27	1,771.95	1,946.50	11.16	0.01
HM2	$d + t$	87.40	1,772.28	1,947.10	11.76	0.00
HM10	$d + (t \times sp)$	90.41	1,785.37	1,966.19	30.85	0.00
HM3	$d + sp$	82.13	1,839.81	2,004.08	68.74	0.00
HM1	d	81.17	1,843.39	2,005.73	70.39	0.00
450-m scale						
HM9	$d + w + sp + (t \times st)$	103.75	1,852.06	2,059.56	0.00	0.60
HM7	$d + (t \times st)$	102.56	1,855.25	2,060.38	0.82	0.40
HM8	$d + w + st$	97.62	1,875.35	2,070.60	11.04	0.00
HM6	$d + t + w + st$	96.34	1,878.70	2,071.39	11.83	0.00
HM5	$d + t + w$	90.52	1,903.40	2,084.45	24.89	0.00
HM2	$d + t$	90.58	1,904.95	2,085.98	26.62	0.00
HM4	$d + t + sp$	91.64	1,902.69	2,086.12	26.56	0.00
HM10	$d + (t \times sp)$	92.93	1,925.06	2,110.92	51.36	0.00
HM1	d	83.35	1,986.80	2,153.51	93.95	0.00
HM3	$d + sp$	84.46	1,984.97	2,153.91	94.35	0.00

differed in their habitat use. Brook Trout showed a greater preference for deep residual pool habitat relative to shallow residual pool habitat and nonpool habitat. Conversely, Brown Trout selected for all three habitat categories similarly (Table 4). Because HM9 included the time of year × stream association interaction, McNuff Branch served as the reference for comparing trout habitat use in the remaining streams. Therefore, Figure 5 represents trout use of shallow and deep residual pool habitats over time in McKinnon Branch and Hunts Run compared with McNuff Branch. The use of residual pool habitat over time did vary across study streams. A gradual decrease in the selection of shallow residual pools over time by trout in McKinnon Branch was detected at the both the 250- and 450-m spatial scales. In contrast, selection of shallow residual pools by trout in Hunts Run increased after mid-December at both the 250- and 450-m scales (Figure 5). Trout in McKinnon Branch exhibited an increase in the use of deep residual pool habitat during mid-October at both the 250- and 450-m scales, followed by a decrease in deep pool use over the remainder of the study. However, Hunts Run trout displayed a decrease in the selection of deep residual pools during early November, followed by an increase in selection during mid-December, at the 250- and 450-m scales (Figure 5).
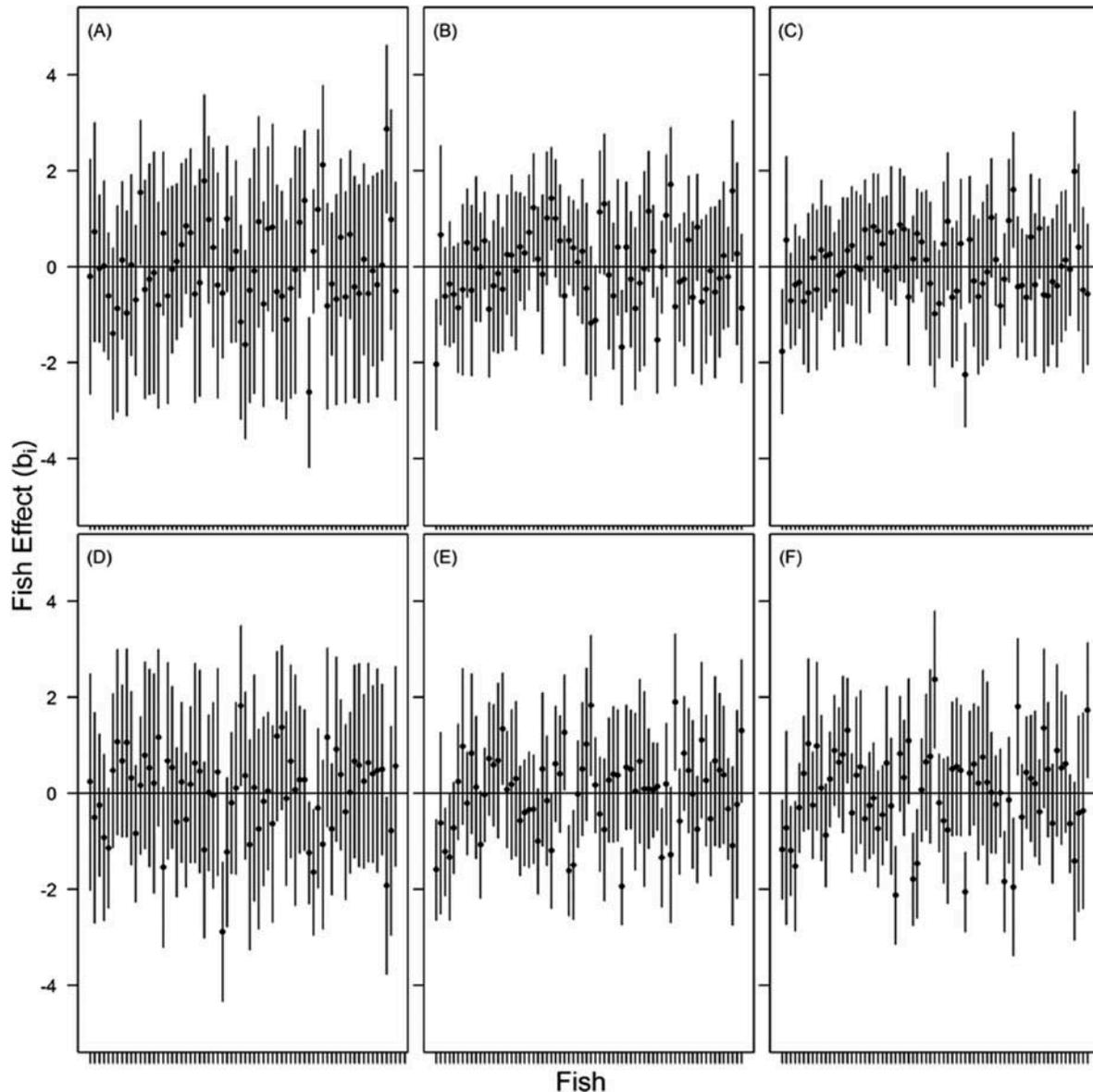
FIGURE 2. Best linear unbiased predictors for individual trout, displaying individual heterogeneity in the use of shallow pool (upper panels) and deep pool (lower panels) habitats (classified according to maximum residual depth) at three spatial scales: **(A), (D)** 50 m; **(B), (E)** 250 m; and **(C), (F)** 450 m. Values are for 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013, in the Hunts Run watershed, Pennsylvania. Each tick mark on the x-axis represents an individual fish; the y-axis depicts the value of the fish effect (b_i; circles = mean ± 95% confidence interval). A b_i value greater than zero indicates that an individual fish used a habitat type more than the population average; a b_i value less than zero indicates that an individual used a habitat type less than the population average.

Log_e(fish weight) was also found to influence habitat use at the 250- and 450-m spatial scales (Figure 6), although the effect was relatively weak and uncertain. The influence of log_e transformed fish weight on trout use of shallow residual pools was nearly linear and demonstrated a flat slope for the 250- and 450-m scales, indicating essentially no effect of fish size on the use of shallow residual pools (Figure 6). However, similar to results for the 50-m scale, there was a positive relationship between the use of deep residual pool habitat and log_e(fish weight) at both the 250- and

450-m scales. Larger trout displayed a greater preference for deep residual pool habitat than did smaller trout (Figure 6).

DISCUSSION

We quantified seasonal residual pool habitat use by Brook Trout and Brown Trout in a stream network. Importantly, we found that inferences regarding habitat use were sensitive to assumptions about how much stream constituted available habitat

TABLE 3. Parameter estimates, SDs, 95% confidence intervals (CIs), and individual fish-specific random effects of the top-ranked discrete-choice model (habitat use model 5) describing habitat use at the 50-m spatial scale for 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013, in the Hunts Run watershed. The reference habitat category was nonpool habitat. The symbol $\hat{\beta}$ represents the estimated species-specific preference for each pool habitat category (defined by maximum residual pool depth); $\widehat{\tau_r^2}$ represents the individual-specific random effect describing variability among individuals in the selection of each pool habitat category. The effects of time and $\log_e$ transformed fish weight were nonparametrically modeled; therefore, those estimates are presented graphically (Figures 3, 4) but are not shown here.

Pool habitat type	$\hat{\beta}$	SD	95% CI	$\widehat{\tau_r^2}$
Shallow pool	3.59	0.358	2.89–4.30	1.67
Deep pool	4.53	0.349	3.84–5.21	1.45

to an individual fish at a given point in time. This scale dependency in habitat use was notable because differences among streams and between trout species were not included in the top-ranked model at the finest scale examined (50 m), whereas among-stream and between-species differences were evident at the two coarsest scales examined (250 and 450 m). The scale-dependent relationships observed here may be partly attributable to the heterogeneous distribution of residual pool habitats within streams. Variation in the distribution of residual pool habitats would potentially result in choice set differences among spatial scales. In addition, habitat use-related covariates may influence habitat selection differently depending on scale. At smaller spatial scales (e.g., 50 m), habitat effects on individual fitness (e.g., growth, survival, fecundity, and reproductive success) have been identified as primary factors limiting populations. At larger spatial scales (e.g., 250 and 450 m), habitat availability has been reported as the primary limiting factor on populations (Rosenfeld and Hatfield 2006); this may include limits placed on populations due to the availability of habitats that are essential for completing certain life history requirements, thus potentially explaining the results we observed. At the smallest spatial scale, fish weight and time of year were identified as factors influencing habitat selection, and in general, body size (weight) is directly related to individual fitness. For example, a positive relationship between fecundity and fish size has been documented in salmonids (Bromage et al. 1990; Downs et al. 1997). In addition, habitat requirements that are necessary to survival in stream salmonids may differ according to fish size, with larger fish generally requiring deeper habitats to avoid predation (Schlosser 1987; Koehn et al. 1994). Lastly, primary factors affecting stream salmonid growth rates include water temperature regime, current velocity, and food availability, all of which typically vary locally (Preall and Ringler 1989). Although our results indicated that fish weight was a factor influencing habitat selection at the 250- and 450-m spatial scales, habitat use was also found to vary over time according to each study stream. Because habitat availability (1) has been identified as the primary factor limiting populations at larger spatial scales and
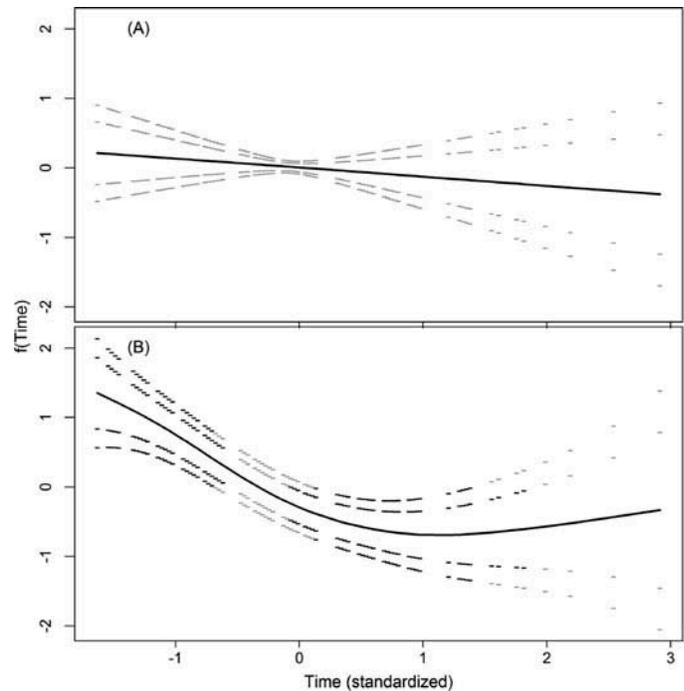

FIGURE 3. Estimated nonparametric effect of time (standardized time of year; see Methods) on trout habitat use at the 50-m spatial scale for **(A)** shallow residual pools and **(B)** deep residual pools (classified according to maximum residual depth) based on habitat use model 5 (see Methods for details) for 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013, in the Hunts Run watershed. Solid lines represent the mean response; dashed lines represent the 80% confidence interval (CI; inner set of lines) and 95% CI (gray shading indicates that the CI overlaps with zero). The x-axis represents standardized time: a value of –1 corresponds to approximately October 12; a value of 1 corresponds to approximately December 20; and a value of 3 corresponds to approximately February 25. The y-axis represents the time effect on trout selection of each pool habitat type. Nonpool habitat was the reference habitat category.

(2) may differ among study streams, it is reasonable to assume that habitat availability would affect habitat use over time differently for each trout species depending on the stream they occupy.

As was expected, Brook Trout and Brown Trout demonstrated an overall greater selection for shallow and deep residual pools relative to nonpool habitats. However, residual pool selection varied temporally at all spatial scales. Similar seasonal variation in habitat use has been documented in other salmonid populations (Cunjak 1996; Gowan and Fausch 1996; Peterson and Fausch 2003; Petty et al. 2005; Young et al. 2010). Factors that may influence seasonal habitat use include temperature (Smith and Kraft 2005; Ficke et al. 2009), flow regime (Ficke et al. 2009), substrate composition (Smith and Kraft 2005), and spawning activities (Swanberg 1997; D'Amelio et al. 2008).

At the 250- and 450-m spatial scales, temporal habitat use by trout also differed among streams, potentially reflecting variation in habitat availability among streams (Young 1995; Jakober et al.
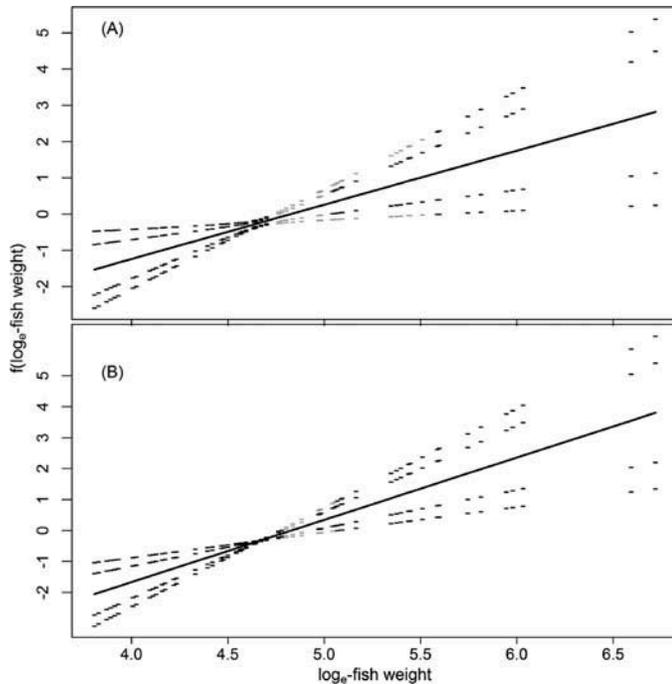
FIGURE 4. Graphical representation of the nonparametric effect of $\log_e$ transformed fish weight on trout habitat use at the 50-m spatial scale for **(A)** shallow residual pools and **(B)** deep residual pools (classified according to maximum residual depth) based on habitat use model 5 (see Methods for details) for 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013, in the Hunts Run watershed. Solid lines represent the mean response; dashed lines represent the 80% confidence interval (CI; inner set of lines) and 95% CI (gray shading indicates that the CI overlaps with zero). The x-axis represents $\log_e$(fish weight). The y-axis represents the effect of $\log_e$(fish weight) on trout selection of each pool habitat type. Nonpool habitat was the reference habitat category.

TABLE 4. Parameter estimates, SDs, 95% confidence intervals (CIs), and individual fish-specific random effects of the top-ranked discrete-choice model (habitat use model 9) describing habitat use at the 250- and 450-m spatial scales for 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013, in the Hunts Run watershed. The reference habitat category for all models was nonpool habitat. Symbols are defined in Table 3. The covariates $\log_e$ transformed fish weight and time of year × stream association interaction were nonparametrically modeled; therefore, those estimates are presented graphically (Figures 5, 6) but are not shown here.

Spatial scale, habitat category, or species	$\hat{\beta}$	SD	95% CI	$\widehat{\tau_r^2}$
250-m scale				
Shallow pool				1.45
Brook Trout	1.39	0.46	0.49 to 2.30	
Brown Trout	0.68	0.43	−0.16 to 1.52	
Deep pool				1.24
Brook Trout	2.79	0.42	1.96 to 3.62	
Brown Trout	0.39	0.39	−0.29 to 1.27	
450-m scale				
Shallow pool				1.37
Brook Trout	0.38	0.43	−0.46 to 1.21	
Brown Trout	0.36	0.41	−0.45 to 1.17	
Deep pool				1.48
Brook Trout	2.03	0.43	1.19 to 2.88	
Brown Trout	0.31	0.41	−0.50 to 1.12	

1998). For example, Young (1995) reported that Brown Trout in different streams varied in their use of woody debris habitat. In addition, among-stream variation in habitat use has been attributed to differences in habitat characteristics, such as discharge, temperature, groundwater inflows, and ice dynamics (Young 1994; Cunjak 1996; Dare et al. 2002). Furthermore, although residual pool habitat did not appear to be limiting given the calculated percentages of each pool category, the amount did vary among study streams. The percentage of residual pool habitat was lowest in McNuff Branch (68% nonpool habitat and 32% residual pool habitat [deep and shallow pools combined]) and greatest in Hunts Run (53% nonpool habitat and 47% residual pool habitat). This variation in residual pool habitat availability may partially explain the differences in temporal habitat selection among study streams. In addition, shallow residual pools were of greater maximum residual depth in Hunts Run (0.10 to <0.39 m) than in McKinnon Branch (0.10 to <0.35 m) or McNuff Branch (0.10 to <0.34 m). This is reasonable because pools with greater maximum residual depths would be more abundant in main-stem reaches than in higher-elevation tributaries.

For McKinnon Branch trout, the use of shallow residual pools decreased over time. Preference was greatest early in the study—around October and November, which would correspond to the spawning period. Mollenhauer et al. (2013) reported similar findings of Brook Trout selection for shallow residual pools during the spawning period. However, those authors also noted that shallow residual pool selection might not be solely a function of residual depth but perhaps could be related to other physical habitat characteristics that are important for spawning (Mollenhauer et al. 2013). For instance, substrate size has been an important factor in redd site selection by Brook Trout and Brown Trout, and coarser substrates are usually associated with shallower depths (Witzel and MacCrimmon 1983; Beriner-Bourgault and Magnan 2002). A different relationship in the temporal selection of shallow residual pools was observed for trout located in Hunts Run than for fish in McKinnon Branch: in Hunts Run, there was an increase in selection for shallow residual pools during mid-December 2012 after the Brown Trout spawning season. This may have been related to the movement of trout from nonpool habitat (consistent with spawning habitat preferences) to shallow residual pools, which were of greater maximum residual depth in Hunts Run than in the other study streams. Several salmonid species have been documented to occupy deep pools during the winter (e.g., Jakober et al. 1998; Harig
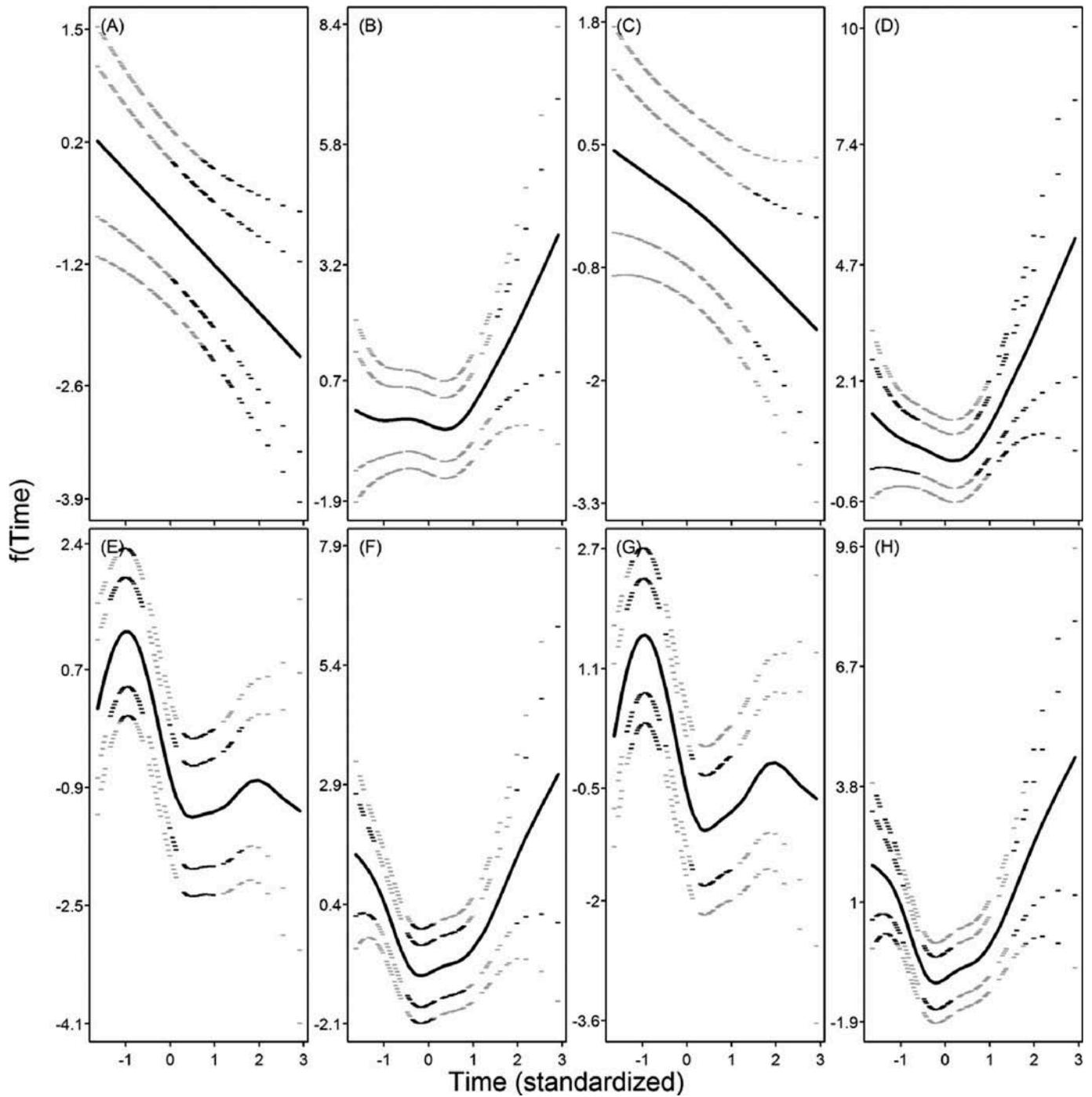
FIGURE 5. Graphical representation of the estimated nonparametric effect of time (standardized time of year; see Methods) on trout use of **(A)**–**(D)** shallow residual pools and **(E)**–**(H)** deep residual pools (classified according to maximum residual depth) at the 250-m (A, B, E, F) and 450-m (C, D, G, H) spatial scales in McKinnon Branch (A, C, E, G) and Hunts Run (B, D, F, H) based on habitat use model 9 (see Methods for details) for 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013. Solid lines represent the mean response; dashed lines represent the 80% confidence interval (CI; inner set of lines) and 95% CI (gray shading indicates that the CI overlaps with zero). The x-axis represents standardized time: a value of –1 corresponds to approximately October 12; a value of 1 corresponds to approximately December 20; and a value of 3 corresponds to approximately February 25. The y-axis represents the time effect on trout selection of each pool habitat type for each stream. Nonpool habitat was the reference habitat category, and McNuff Branch was used as the reference stream to which pool habitat use in McKinnon Branch and Hunts Run was compared.
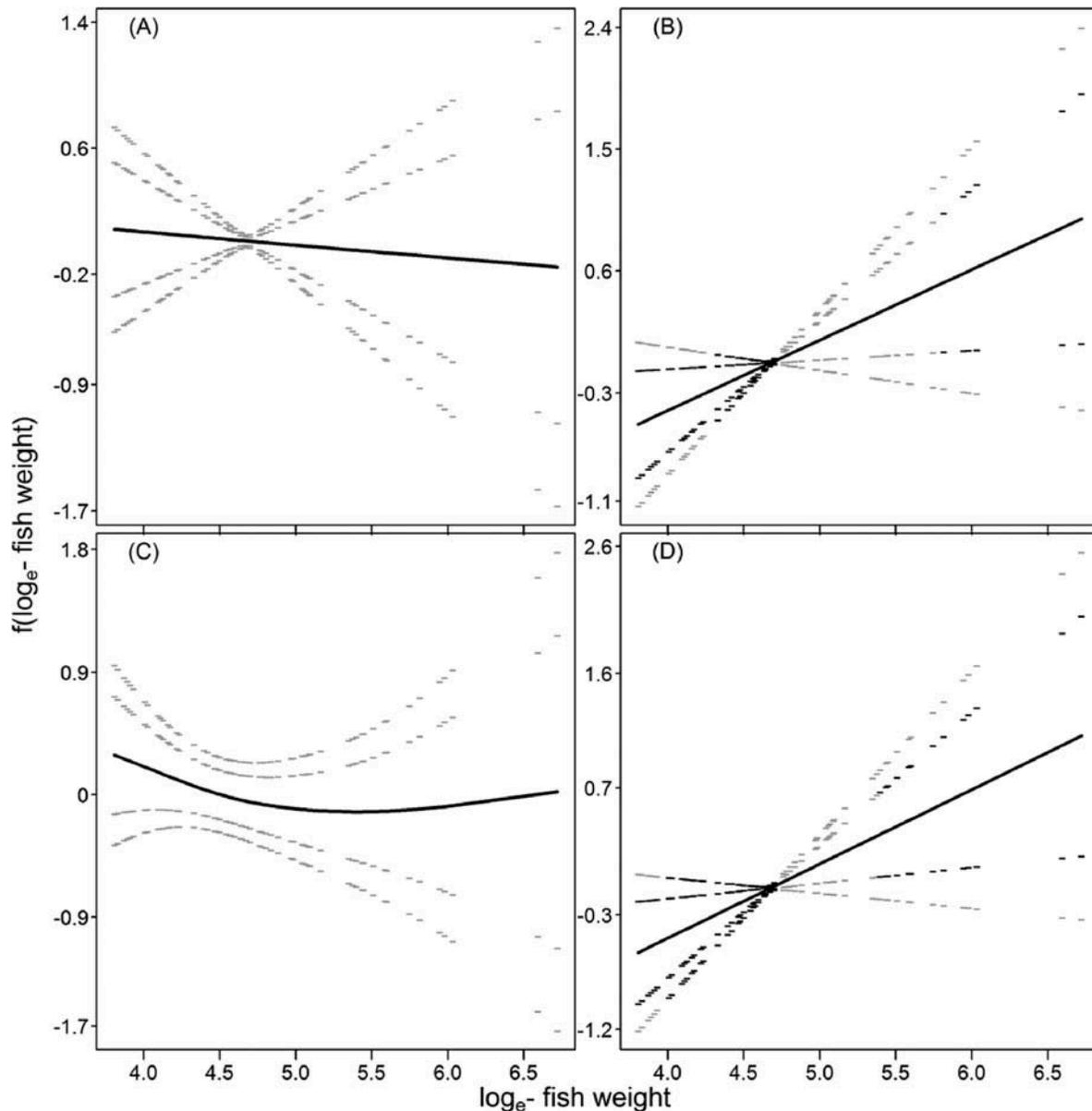
FIGURE 6. Estimated nonparametric effect of $\log_e$ transformed fish weight on trout use of **(A), (C)** shallow residual pools and **(B), (D)** deep residual pools (classified according to maximum residual depth) at the 250-m (A, B) and 450-m (C, D) spatial scales based on habitat use model 9 (see Methods for details) for 31 Brook Trout and 40 Brown Trout that were radio-tracked between September 16, 2012, and February 25, 2013, in the Hunts Run watershed. Solid lines represent the mean response; dashed lines represent the 80% confidence interval (CI; inner set of lines) and 95% CI (gray shading indicates that the CI overlaps with zero). The x-axis represents $\log_e$(fish weight). The y-axis represents the effect of $\log_e$(fish weight) on trout selection of each pool habitat type. Nonpool habitat was the reference habitat category.

and Fausch 2002; Lindstrom and Hubert 2004). Therefore, increased selection for shallow residual pools by Hunts Run trout may reflect winter habitat selection.

Trout selection of deep residual pools during the winter months was also observed in Hunts Run. Deeper habitats are typically associated with a lack of anchor ice (Jakober et al. 1998), lower water velocities (Cunjak and Power 1986; Clapp et al. 1990), and greater overhead cover (Cunjak and Power

1986), all of which are considered favorable to overwintering salmonids. In contrast, the selection of deep residual pools differed for trout that were located in McKinnon Branch. During mid-October 2012, greater selection for deep residual pools compared with nonpool habitat was apparent, followed by a decrease in deep pool selection through November. Although trout in McKinnon Branch were also selecting for shallow residual pools during that time, possibly

corresponding to spawning habitat preferences, four trout were observed spawning in the tailouts of deep residual pools. Jakober et al. (1998) reported similar findings for the spawning activity of Bull Trout *Salvelinus confluentus*. Pool tailouts can be associated with coarser substrates and increased flow, thus providing suitable spawning habitat for Brook Trout and Brown Trout. In addition, during low-flow conditions like those occurring in mid-October, spawning habitat may be reduced, thereby forcing stream salmonids to spawn in greater depths that would not be considered suitable under higher flow conditions (Belica 2007). Therefore, the mechanisms driving trout selection of deep residual pools in McKinnon Branch during that time may have been more complex.

Another factor influencing habitat selection at the 250- and 450-m spatial scales was species association—that is, differences in habitat selection between the two trout species. Brook Trout selected for deep residual pools more than shallow residual pools or nonpool habitat, whereas Brown Trout showed little habitat preference, selecting for all three habitat categories similarly. This was contrary to expectations given the Brown Trout's proposed competitive superiority over Brook Trout in preferred habitats (Fausch and White 1981; DeWald and Wilzbach 1992). Furthermore, these results are contrary to previous studies describing the Brown Trout's daytime preference for deep pools (O'Connor and Rahel 2009). We observed some predation on Brook Trout by what appeared to be avian or wading predators; based on this, we hypothesize that deep residual pools provided more favorable refuge from avian and wading predators than shallow residual pools or nonpool habitats (Schlosser 1987; Koehn et al. 1994). Furthermore, physical habitat factors in addition to residual pool depth may be acting on habitat selection.

Habitat selection by some stream fishes has been shown to be size dependent, with larger fish typically being associated with deeper habitats and smaller fish being associated with shallower habitats (Grossman and Freeman 1987; Schlosser 1987; Koehn et al. 1994). This relationship has been partly attributed to an increased risk of predation by both avian and terrestrial predators on larger individual fish occupying shallower habitats (Schlosser 1987; Koehn et al. 1994). A similar relationship for the use of deep residual pools was observed in this study, as increased selection of deep pools by larger Brook Trout and Brown Trout occurred at all three spatial scales. However, the relationship between fish weight and the use of shallow residual pools was scale dependent: there was essentially no effect of fish weight on shallow residual pool use at the 250- and 450-m spatial scales, whereas there was a positive effect of fish weight at the 50-m scale. This scale-dependent relationship may reflect factors that act on fish differently at differing spatial scales. For example, agonistic interactions usually dominated by larger individuals for foraging sites but not refuge sites have been documented (Bachman 1984). Therefore, increased selection for shallow pool habitat by larger trout may have been the result of competitive interactions acting on fish more at the 50-m spatial scale than at the 250- and 450-m scales.

The random effects in the models indicated little variability among individuals in the use of shallow and deep residual pools; this result suggests that seasonal habitat requirements may have had a strong influence on Brook Trout and Brown Trout habitat use. Increased variability among individuals would indicate that factors such as food availability, thermal preference, and current velocity (Preall and Ringler 1989; Jakober et al. 1998) are acting on individuals differently. Additionally, interspecific and intraspecific competition or interactions could also affect among-individual variability in habitat selection (Fausch and White 1981; Cunjak and Power 1986).

Overall, habitat use by Brook Trout and Brown Trout was largely temporally driven but varied depending on the spatial scale of available habitat. The variation in temporal habitat selection among study streams highlights the complexity of seasonal habitat use by Brook Trout and Brown Trout and indicates that factors acting on individuals may influence habitat selection differently depending on the scale of available habitat. The present results have implications for future Brook Trout management and conservation efforts, as conserving existing populations may require an understanding of the scale at which each population should be managed (i.e., single stream reach or across a watershed).

ACKNOWLEDGMENTS

REFERENCES

Ayllón, D., A. Almodóvar, G. G. Nicola, and B. Elvira. 2010. Ontogenetic and spatial variations in Brown Trout habitat selection. Ecology of Freshwater Fish 19:420–432.

Ayllón, D., G. G. Nicola, I. Parra, B. Elvira, and A. Almodóvar. 2014. Spatio-temporal habitat selection shifts in Brown Trout populations under contrasting natural flow regimes. Ecohydrology 7:569–579.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery Brown Trout in a stream. Transactions of the American Fisheries Society 113:1–32.

Baird, O. E., and C. C. Krueger. 2003. Behavioral thermoregulation of Brook and Rainbow trout: comparison of summer habitat use in an Adirondack river, New York. Transactions of the American Society 132:1194–1206.

Baird, O. E., C. C. Krueger, and D. C. Josephson. 2006. Growth, movement, and catch of Brook, Rainbow, and Brown trout after stocking into a large, marginally suitable Adirondack river. North American Journal of Fisheries Management 26:180–189.

Baker, J. P., J. Van Sickle, C. J. Gagen, C. R. DeWalle, W. E. Sharpe, R. F. Carline, B. P. Baldigo, P. S. Murdoch, D. W. Bath, W. A. Krester, H. A. Simonin, and P. J. Wigington Jr. 1996. Episodic acidification of small streams in the northeastern United States: effects on fish populations. Ecological Applications 6:422–437.

Baxter, C. V., and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by Bull Trout (Salvelinus confluentus). Canadian Journal of Fisheries and Aquatic Sciences 57:1470–1481.

Belica, L. 2007. Brown Trout (Salmo trutta): a technical conservation assessment. U.S. Forest Service, Rocky Mountain Region, Golden, Colorado.

Bernier-Bourgault, I., and P. Magnan. 2002. Factors affecting redd site selection, hatching, and emergence of Brook Charr, Salvelinus fontinalis, in an artificially enhanced site. Environmental Biology of Fishes 64:333–341.

Bromage, N., P. Hardiman, and J. Jones. 1990. Fecundity, egg size, and total egg volume differences in 12 stocks of Rainbow Trout, Oncorhynchus mykiss (Richardson). Aquaculture Research 21:269–284.

Clapp, D. F., R. D. Clark Jr., and J. S. Diana. 1990. Range, activity, and habitat of large, free-ranging Brown Trout in a Michigan stream. Transactions of the American Fisheries Society 119:1022–1034.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident Brook Trout (Salvelinus fontinalis) and Brown Trout (Salmo trutta). Canadian Journal of Fisheries and Aquatic Sciences 43:1970–1981.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Sciences 53:267–282.

D'Amelio, S., J. M. Mucha, R. B. Mackereth, and C. C. Wilson. 2008. Tracking coaster Brook Trout to their sources: combining telemetry and genetic profiles to determine source populations. North American Journal of Fisheries Management 28:1343–1349.

Dare, M. R., W. A. Hubert, and K. G. Gerow. 2002. Changes in habitat availability and habitat use and movement by two trout species in response to declining discharge in a regulated river during winter. North American Journal of Fisheries Management 22:917–928.

Davis, L. A., T. Wagner, and M. L. Bartron. 2015. Spatial and temporal movement dynamics of Brook Salvelinus fontinalis and Brown trout Salmo trutta. Environmental Biology of Fishes 98:2049–2065.

DeWald, L., and M. A. Wilzbach. 1992. Interactions between native Brook Trout and hatchery Brown Trout: effects on habitat use, feeding, and growth. Transactions of the American Fisheries Society 121:287–296.

Downs, C. C., R. G. White, and B. B. Shepard. 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of Westslope Cutthroat Trout. North American Journal of Fisheries Management 17:95–92.

EBTJV (Eastern Brook Trout Joint Venture). 2011. Conserving the eastern Brook Trout: action strategies. EBTJV, Sanbornton, New Hampshire.

Fausch, K. D., and R. J. White. 1981. Competition between Brook Trout (Salvelinus fontinalis) and Brown Trout (Salmo trutta) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 3:1220–1227.

Feist, B. E., E. A. Steel, G. R. Pess, and R. E. Bilby. 2003. The influence of scale on salmon habitat priorities. Animal Conservation 6:271–282.

Ficke, A. D., D. P. Peterson, and B. Janowsky. 2009. Brook Trout (Salvelinus fontinalis): a technical conservation assessment. U.S. Forest Service, Rocky Mountain Region, Golden, Colorado.

Gowan, C., and K. D. Fausch. 1996. Mobile Brook Trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370–1381.

Grossman, G. D., and M. C. Freeman. 1987. Microhabitat use in a stream assemblage. Journal of Zoology 212:151–176.

Hakala, J. P., and K. J. Hartman. 2004. Drought effect on stream morphology and Brook Trout (Salvelinus fontinalis) populations in forested headwater streams. Hydrobiologia 515:203–213.

Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated Cutthroat Trout populations. Ecological Applications 12:535–551.

Harrelson, C. C., C. L. Rawlins, and J. P. Potyondy. 1994. Stream channel reference sites: an illustrated guide to field technique. U.S. Forest Service General Technical Report RM-245.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by Bull Trout and Cutthroat Trout in Montana headwater streams. Transactions of the American Fisheries Society 127:223–235.

Jones, N. E., and W. M. Tonn. 2004. Resource selection functions for age-0 Arctic Grayling (Thymallus arcticus) and their application to stream habitat compensation. Canadian Journal of Fisheries and Aquatic Sciences 61:1736–1746.

Kneib, R., F. Knauer, and H. Küchenhoff. 2011. A general approach to the analysis of habitat selection. Environmental and Ecological Statistics 18:1–25.

Koehn, J. D., N. A. O'Connor, and P. D. Jackson. 1994. Seasonal and size related variation in microhabitat use by a southern Victorian stream fish assemblage. Australian Journal of Marine and Freshwater Research 45:1353–1366.

Lindstrom, J. W., and W. A. Hubert. 2004. Ice processes affect habitat use and movements of adult Cutthroat Trout and Brook Trout in a Wyoming foothills stream. North American Journal of Fisheries Management 24:1341–1352.

Lisle, T. E. 1987. Using "residual depths" to monitor pool depths independently of discharge. U.S. Forest Service Research Note PSW-394.

Malmqvist, B., and S. Rundle. 2002. Threats to running water ecosystems of the world. Environmental Conservation 29:134–153.

Mollenhauer, R., T. Wagner, M. V. Kepler, and J. A. Sweka. 2013. Fall and early winter movement and habitat use of wild Brook Trout. Transactions of the American Fisheries Society 142:1167–1178.

Mossop, B., and M. J. Bradford. 2006. Using thalweg profiling to assess and monitor juvenile salmon (Oncorhynchus spp.) habitat in small streams. Canadian Journal of Fisheries and Aquatic Sciences 63:1515–1525.

Muhlfeld, C. C., and B. Marotz. 2005. Seasonal movement and habitat use by subadult Bull Trout in the upper Flathead River system, Montana. North American Journal of Fisheries Management 25:797–810.

Neely, B. C., M. A. Pegg, and G. E. Mestl. 2010. Seasonal resource selection by Blue Suckers Cycleptus elongatus. Journal of Fish Biology 76:836–851.

Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile Coho Salmon (Oncorhynchus kisutch) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783–789.

O'Connor, R. R., and F. J. Rahel. 2009. A patch perspective on summer habitat use by Brown Trout Salmo trutta in a high plains stream in Wyoming, USA. Ecology of Freshwater Fish 18:473–480.

PADCNR (Pennsylvania Department of Conservation and Natural Resources). 2010. Brook Trout (Salvelinus fontinalis) conservation plan. PADCNR, Harrisburg. Available: www.dcnr.state.pa.us/cs/groups/public/documents/document/dcnr_20027100.pdf. (December 2013).

Peterson, R. H., and K. D. Fausch. 2003. Upstream movement by nonnative Brook Trout (Salvelinus fontinalis) promotes invasion of native Cutthroat Trout (Oncorhynchus clarki) habitat. Canadian Journal of Fisheries and Aquatic Sciences 60:1502–1516.

Petty, J. T., J. L. Hansbarger, B. M. Huntsman, and P. M. Mazik. 2012. Brook Trout movement in response to temperature, flow, and thermal refugia with a complex Appalachian riverscape. Transactions of the American Fisheries Society 141:1060–1073.

Petty, J. T., P. L. Lamothe, and P. M. Mazik. 2005. Spatial and seasonal dynamics of Brook Trout populations inhabiting a central Appalachian watershed. Transactions of the American Fisheries Society 134:572–587.

Preall, R. J., and N. H. Ringler. 1989. Comparison of actual and potential growth rates of Brown Trout (*Salmo trutta*) in natural streams based on bioenergetic models. Canadian Journal of Fisheries and Aquatic Sciences 46:1067–1076.

Rosenfeld, J. S., and T. Hatfield. 2006. Information needs for assessing critical habitat of freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences 63:683–698.

Saiget, D. A., M. R. Sloat, and G. H. Reeves. 2007. Spawning and movement behavior of migratory Coastal Cutthroat Trout on the western Copper River delta, Alaska. North American Journal of Fisheries Management 27:1029–1040.

Schlosser, I. J. 1987. The role of predation in age- and size-related habitat use by stream fishes. Ecology 63:307–313.

Smith, T. A., and C. E. Kraft. 2005. Stream fish assemblages in relation to landscape position and local habitat variables. Transactions of the American Fisheries Society 134:430–440.

Solazzi, M. F., T. E. Nickelson, S. L. Johnson, and J. D. Rodgers. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 57:906–914.

Stranko, S. A., A. J. Becker, R. H. Hilderbrand, P. T. Jacobson, R. P. Morgan, E. S. Perry, A. Roseberry-Lincoln, and M. W. Staley. 2008. Brook Trout declines with land cover and temperature changes in Maryland. North American Journal of Fisheries Management 28:1223–1232.

Swanberg, T. 1997. Movements and habitat use by fluvial Bull Trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126:735–746.

Witzel, L. D., and H. R. MacCrimmon. 1983. Redd-site selection in Brook Trout and Brown Trout in southwestern Ontario streams. Transactions of the American Fisheries Society 112:761–771.

Young, M. K. 1994. Mobility of Brown Trout in south-central Wyoming streams. Canadian Journal of Zoology 72:2078–2083.

Young, M. K. 1995. Telemetry-determined diurnal positions of Brown Trout (*Salmo trutta*) in two south-central Wyoming streams. American Midland Naturalist 133:264–273.

Young, M. K. 1996. Summer movements and habitat use by Colorado River Cutthroat Trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. Canadian Journal of Fisheries and Aquatic Sciences 43:1403–1408.

Young, R. G., J. Wilkinson, J. Hay, and J. W. Hayes. 2010. Movement and mortality of adult Brown Trout in the Motupiko River, New Zealand: effects of water temperature, flow and flooding. Transactions of the American Fisheries Society 139:137–146.