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ARTICLE

Brook Trout Movement in Response to Temperature, Flow, and Thermal Refugia within a Complex Appalachian Riverscape

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Abstract

We quantified movements of brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* in a complex riverscape characterized by a large, open-canopy main stem and a small, closed-canopy tributary in eastern West Virginia, USA. Our objectives were to quantify the overall rate of trout movement and relate movement behaviors to variation in streamflow, water temperature, and access to coldwater refugia. The study area experienced extremely high seasonal, yearly, and among-stream variability in water temperature and flow. The relative mobility of brook trout within the upper Shavers Fork watershed varied significantly depending on whether individuals resided within the larger main stem or the smaller tributary. The movement rate of trout inhabiting the main stem during summer months (50 m/d) was an order of magnitude higher than that of tributary fish (2 m/d). Movement rates of main-stem-resident brook trout during summer were correlated with the maximum water temperature experienced by the fish and with the fish's initial distance from a known coldwater source. For main-stem trout, use of microhabitats closer to cover was higher during extremely warm periods than during cooler periods; use of microhabitats closer to cover during warm periods was also greater for main-stem trout than for tributary inhabitants. Main-stem-resident trout were never observed in water exceeding 19.5°C. Our study provides some of the first data on brook trout movements in a large Appalachian river system and underscores the importance of managing trout fisheries in a riverscape context. Brook trout conservation in this region will depend on restoration and protection of coldwater refugia in larger river main stems as well as removal of barriers to trout movement near tributary and main-stem confluences.

Biological, chemical, and physical factors exist within lotic ecosystems as a complex patchwork at multiple spatial scales, a phenomenon that is increasingly referred to as a riverscape (Fausch et al. 2002). For example, depth, current velocity, and food abundance can vary dramatically within a relatively small area in intermediate-gradient streams (Petty and Grossman 2010). Physical and biological conditions in streams can change on a temporal basis as well (Hildrew and Giller 1994). In particular, streamflow, water temperature, and

invertebrate prey densities may vary on a yearly, seasonal, daily, and even hourly basis. Given these complexities, the ability of individual fish to maximize survival, reproduction, and growth rates in stream ecosystems is strongly dependent on their ability to respond to spatial and temporal variability in habitat conditions through movement (Berman and Quinn 1991; Torgersen et al. 1999; Fausch et al. 2002; Gowan and Fausch 2002; Petty and Grossman 2004, 2010; Young et al. 2010).

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Past studies of trout movement have focused on questions about how extensively trout move, and many early researchers suggested that stream-dwelling species are sedentary. Gerking (1953, 1959) proposed that stream fishes generally lead a sedentary life style, interrupted only by unusual or specialized behaviors, such as dispersal of fry, various ontogenetic shifts related to habitat use, and small-scale diel movements between feeding and resting areas. Bachman's (1984) research reinforced the idea that many stream fishes exhibit strong site fidelity, and the "restricted movement paradigm" became a cornerstone of our understanding of stream fish behavior (Gowan et al. 1994).

Movement by stream fishes is now understood to play a larger part in their life histories, allowing them to utilize a wide array of habitat types across a range of spatial scales (Schlosser 1991, 1995; Northcote 1997; Torgersen et al. 1999; Petty and Grossman 2004, 2010; Young et al. 2010). Researchers have found that members of the Salmonidae family (Curry et al. 2002)—particularly the brook trout *Salvelinus fontinalis* (Rodríguez 2002)—exhibit high levels of movement and adaptive plasticity in habitat use. Rodríguez (2002) emphasized that the scale of the investigation and nature of the study often dictate whether fish movement is deemed "extensive" by researchers. Furthermore, movement behaviors typically are not constant but rather are carried out as punctuated events (Petty and Grossman 2004), and fish populations may comprise both mobile and sedentary individuals (Skalski and Gilliam 2000; Rodríguez 2002; Hilderbrand and Kershner 2004; Petty and Grossman 2004; Morinville and Rasmussen 2006).

Mechanisms that have been shown to influence fish movement strategies include both biotic and abiotic factors (Riley et al. 1992). Movement is an important tactic for thermoregulation of coldwater species (Goniaea et al. 2006; Keefer et al. 2009; McCullough et al. 2009; Young et al. 2010). Additionally, differences in mobility strategies among individuals within a salmonid species may be directly influenced by stream velocity, where faster-moving waters support more streamlined and mobile fish (Morinville and Rasmussen 2006; Morinville and Rasmussen 2008). Biotic components, such as the ability to exploit patchily distributed resources, also have been shown to be important determinants of fish movement (Hughes 1998; Rosenfeld et al. 2005; Petty and Grossman 2010). For example, Petty and Grossman (2010) showed that movements of mottled sculpin *Cottus bairdii* were influenced by changes in the distribution of invertebrate prey and competition for high-quality feeding territories.

The ability to assess habitat quality and to move between different habitat types as needed is critical for trout populations (Torgersen et al. 1999; Fausch et al. 2002; Gowan and Fausch 2002; Young et al. 2010). Nevertheless, few studies have explicitly sought to link trout movements to the presumed causal mechanisms of spatial and temporal variability in habitat quality, especially over multiple seasons, within both main-stem lotic systems and associated smaller tributaries (Maki-Petays et al. 1997; Bunnell et al. 1998; Burrell et al. 2000;

Bramblett et al. 2002). Given the importance of movement within spatially and temporally complex riverscapes, we conducted a study of trout movement and habitat use in the upper Shavers Fork of the Cheat River, West Virginia. The overriding objective of our research was to contrast the behaviors of trout residing in two very different types of habitat: small, cold, low-productivity tributaries and large, warm, high-productivity main stems (Petty et al. 2005). Specifically, we (1) quantified spatial, temporal, and species-related (brook trout versus brown trout *Salmo trutta*) differences in trout movement behaviors, (2) correlated variation in trout movement rates with changes in thermal conditions and the distribution of coldwater sources, and (3) tested for shifts in trout microhabitat use in response to changing thermal conditions within the watershed.

STUDY AREA

The upper Shavers Fork is a large (i.e., basin area > 150 km²), high-elevation (originates at 1,500 m) watershed located in the central Appalachian Mountains of eastern West Virginia (Pocahontas and Randolph counties; Figure 1). The Shavers Fork is part of the Cheat River drainage, flowing north to its confluence with the Monongahela River. We conducted fieldwork within the main-stem upper Shavers Fork and a second-order tributary, Rocky Run. The study area was located entirely within the Monongahela National Forest in eastern West Virginia. Land cover is dominated by a mixed deciduous–coniferous forest.

Natural variation in bedrock geology and stream size produces a high degree of variability in water chemistry and habitat characteristics in this watershed (Petty et al. 2003, 2005; Petty and Thorne 2005). Consequently, the physical and biological characteristics of the upper Shavers Fork and Rocky Run study areas differed substantially (Table 1). The main-stem upper Shavers Fork is relatively wide and shallow, has a low gradient and an open canopy, is warmer and more productive, and possesses a more diverse fish assemblage than Rocky Run and other tributaries (Bopp 2002). Rocky Run is higher gradient and narrow, has a high occurrence of large boulders and large woody debris (LWD), has a dense tree canopy, and is cooler and less productive than the main stem (Table 1). Although many small streams in the watershed are acidic as a result of acid precipitation (Petty and Thorne 2005; Petty et al. 2005), both the main stem and Rocky Run are generally circumneutral (i.e., they possess a base flow pH between 6.6 and 7.0; McClurg et al. 2007). Fish assemblages in the upper Shavers Fork are typical of Appalachian streams and include brook trout, brown trout, rainbow trout *Oncorhynchus mykiss*, rosyface shiner *Notropis rubellus*, rosieside dace *Clinostomus funduloides*, western blacknose dace *Rhinichthys obtusus*, longnose dace *R. cataractae*, central stoneroller *Campostoma anomalum*, fantail darter *Etheostoma flabellare*, mottled sculpin, northern hog sucker *Hypentelium nigricans*, and creek chub *Semotilus atromaculatus* (Petty et al. 2005).

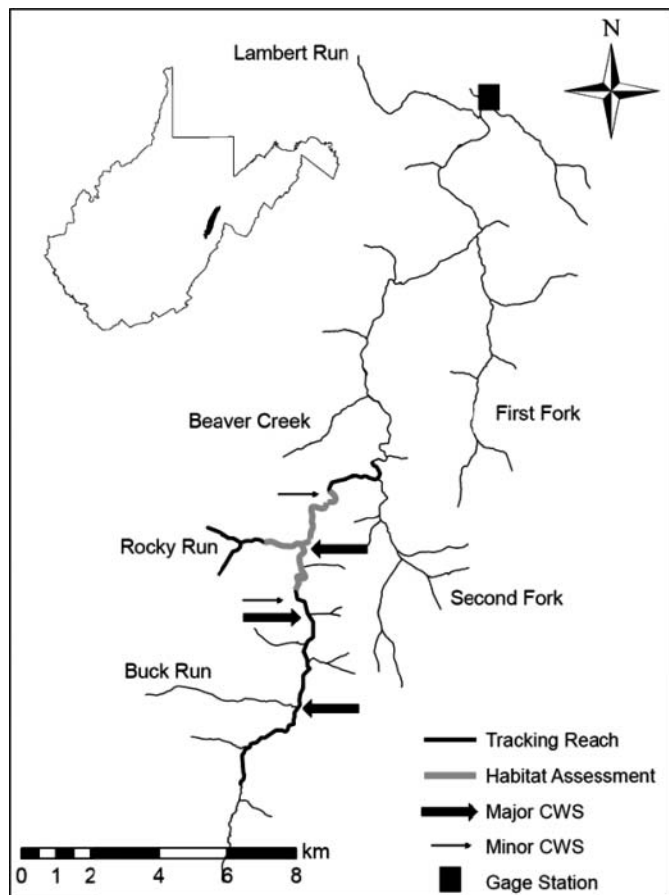


FIGURE 1. Map of the study area within the upper Shavers Fork watershed in eastern West Virginia. Streamflow is from south to north. The tracking reach extended approximately 8 km along the Shavers Fork main stem and an additional 4 km to the headwaters of Rocky Run. Microhabitat availability was sampled within a subset of this area, and several minor and major coldwater sources (CWSs) were identified along the main stem.

METHODS

Temperature and streamflow monitoring.—An 8-km study reach was delineated on the upper Shavers Fork main stem, and a 4-km reach was delineated on Rocky Run. Wooden stakes with fluorescent tips were placed along the study reaches every 50 m on the main stem and every 25 m on Rocky Run. Seven continuous temperature loggers (HOBO; Onset Computer Corp., Bourne, Massachusetts) were anchored within the main-stem study area, and three loggers were anchored in the tributary. Spacing of the loggers was arranged to capture spatial and temporal variation in ambient water temperature throughout the study area. Shavers Fork streamflow was monitored at the U.S. Geological Survey gauging station located at Cheat Bridge, West Virginia, approximately 25 km downstream of our study area (Figure 1).

Trout capture and tracking.—This study was conducted over a period of 60–70 d during three separate seasons: summer 2000, fall 2000, and summer 2001. The summer sampling seasons were from June 5 to August 15 of each year; the fall season extended from September 5 to November 15. In summer 2000, only native brook trout were sampled. Wild brown trout were added to the study design in fall 2000 and summer 2001. All fish were captured within the study region by using electrofishing techniques and were returned as close to their capture location as possible.

Once captured, trout received internal radio transmitters that were surgically implanted by following protocols derived from multiple sources (Courtois 1981; Ross and Kleiner 1982; Winter 1983; Swanberg 1997). Transmitters included an external antenna that was trimmed to approximately 250 mm. Trout were handled according to the guidelines of West Virginia University's Animal Care and Use Committee (Protocol Number 9801-12). Clove oil was used as an anesthetic and antiseptic for the surgery via the procedure outlined by Anderson et al. (1997).

TABLE 1. Summary statistics (means with ranges in parentheses) describing the Shavers Fork main stem and its tributary, Rocky Run, in West Virginia (Petty et al. 2005).

Variable	Rocky Run	Shavers Fork
Basin area (km ²)	6.7	35.2
Wetted width (m)	8.3 (6.4–9.0)	21.2 (16.1–27.8)
Canopy cover (%)	70 (63–85)	24 (20–32)
pH	6.4 (5.6–7.2)	6.7 (6.2–7.4)
Alkalinity (mg/L CaCO ₃)	11.2 (4.0–22.8)	51.1 (22–136)
Benthic macroinvertebrate density (individuals/m ²)	2,770 (1,800–3,750)	4,866 (2,900–6,100)
Benthic macroinvertebrate biomass (mg/m ²)	220 (80–550)	493 (300–700)
Brook trout density (fish/m)	0.60 (0.23–1.02)	0.06 (0.025–0.10)
Brook trout age structure		
Percent young of the year	30	14
Percent small adults (<150 mm)	54	46
Percent large adults (>150 mm)	16	40
Fish species richness	6	18

During each season, three to five fish were held to ensure proper postsurgery recuperation, but no fish was held for longer than 24 h after surgery. Transmitters (MBFT series; Lotek Industries) weighed 2.0 g (expected battery life = 47 d) and 1.8 g (expected battery life = 34 d), with signals transmitted at frequencies every 0.010 MHz between 149.540 and 150.720 MHz. We restricted transmitter implantation to fish larger than 72 g (~175–180 mm) to comply with the “modified Winter rule,” which states that the transmitter weight should be no more than 2.5% of fish body weight (Winter 1983; Swanberg 1997). To maximize battery life, transmitters were programmed to operate in a cycle of 1 d on, 1 d off, with alternating hours of on and off during the “on” days.

Twenty-eight trout were given implanted transmitters and released during each season, for a total of 84 trout used during the study. In summer 2000, 8 brook trout were released into Rocky Run and 20 brook trout were released into the main stem. During summer 2001, 5 brook trout were released into Rocky Run, 15 brook trout were released into the main stem, and 8 brown trout were released into the main stem. Release of fish with transmitters during summer was weighted in favor of main-stem brook trout because we were primarily interested in brook trout movements in the larger water body and we were concerned about the loss of tagged trout in the main stem. In addition, results from the summer 2000 season indicated that brook trout residing in Rocky Run exhibited very little interindividual variation in movement behavior. In fall 2000, we released 16 brook trout into Rocky Run, 2 brook trout into the main stem, and 10 brown trout into the main stem. Prior to the implantation of transmitters for the fall season, larger brook trout had generally moved from the main stem into nearby tributaries to spawn. Consequently, we focused on movements of brown trout in the main stem and brook trout in the tributary during the fall 2000 study period.

To ensure full recovery and resumption of normal behaviors in study fish, official tracking did not begin until 10 d after the release of tagged fish. All at-large fish were located by using a Lotek SRX 600 data logger receiver at least twice per week in each season between 0600 and 2100 hours, thus completing one “track.” We located trout by walking parallel to and within 50 m of the stream bank until a signal was detected (Young 1995). Each located fish was visually identified to ensure that the transmitter was still associated with a living individual (Burrell et al. 2000). Throughout each track, an exhaustive effort was made to locate all tagged trout throughout the watershed. If a fish was not located during three consecutive tracks, it was considered to have been lost from predation, harvest, or emigration. To minimize the effect of time of day on habitat use and movement, different starting points were chosen for each daily track to ensure that all tagged trout were encountered at varying times throughout the day (*sensu* Petty and Grossman 2004). Tracking continued for up to 71 d in each season. Most transmitters had ceased functioning by day 60.

Diel (24-h) tracks of trout movement and habitat use were included in our sampling to investigate seasonal shifts in diel movement patterns (Burrell et al. 2000). Four trout from each study area (i.e., main stem versus tributary) were monitored over a 24-h period, with locations identified every other hour for each tagged trout. For each species, we conducted three separate diel tracks per season (i.e., at the beginning, in the middle, and at the end of the season). Preliminary analysis of the diel tracks failed to indicate a significant difference in movement behaviors over time. For brevity, results from the nighttime observations are not included.

Trout microhabitat use and movement.—Upon relocating a trout, we collected the following information: geographic location based on the stakes placed along the experimental reaches, time of day, water clarity (low, moderate, or high), hydraulic channel unit type (e.g., pool, riffle, or run; Petty et al. 2003), and physical microhabitat variables at the focal point of the observed trout (Hansbarger et al. 2010). Microhabitat variables included focal point temperature (°C), pH, water depth (cm), bottom current velocity (m/s), average current velocity (m/s), focal point current velocity (m/s), maximum current velocity (m/s) within 60 cm (Fausch and White 1981), distance to cover (m), cover type used, and distance to a known coldwater source (m). Current velocities were measured with a Marsh-McBirney flowmeter. Cover was defined as any object that was capable of concealing a 15-cm fish and consisted of undercut banks, large boulders, and LWD (Flebbe and Dolloff 1995). Coldwater sources included tributary confluences as well as visually identified lateral groundwater seeps along the banks of the main-stem channel. Prior to taking the microhabitat use measurements, we observed trout for a few minutes to note their general location and activity. We substituted a reading of 10 cm from the bottom for an adjusted focal point whenever instream turbidity prevented us from determining the exact location of individual trout (Young 1995). Trout were apparently not bothered by the sampling procedures, as they were often observed to re-establish their feeding positions a short time after the series of microhabitat measurements was taken. Similar behaviors have been noted for cutthroat trout *O. clarkii* (Young 1995) and for brown trout (Bunnell et al. 1998).

Microhabitat availability.—We sampled microhabitat availability by using protocols from Simonson et al. (1994) and Petty et al. (2003). Instream flows averaged between 1.3 and 1.4 m³/s during the majority of the time at large for tagged trout, and microhabitat availability sampling was conducted at similar flows in summer 2001. Rocky Run was considered a small tributary based on wetted stream width measurements (mean stream width [MSW] = 4.9 m; Simonson et al. 1994). Microhabitat measurements were taken at five evenly distributed points along transects spaced every 3 MSWs. In total, 28 transects were distributed across a 405-m-long study reach on Rocky Run that began approximately 100 m upstream of the tributary’s mouth; this resulted in the sampling of 140 microhabitat quadrats in

Rocky Run. The Shavers Fork main stem was considered a large stream based on wetted stream width (MSW = 14 m). Microhabitat was sampled at five evenly spaced locations along 80 transects spaced every 2 MSWs. The main-stem study reach was 2,212 m long, with a total of 400 microhabitat quadrats sampled. The midpoint of the main-stem study reach was located at the Rocky Run confluence. A greater sampling area was needed in the main stem in order to encompass the range of movements exhibited by trout. At each location along a sample transect, we measured the following variables: average current velocity, bottom current velocity, water depth, distance to the nearest cover item, and cover item type.

Statistical analyses.—We used streamflow and temperature data to calculate mean daily flow (m^3/s); mean daily temperature; maximum daily temperature; average daily maximum temperature (DMT); the mean and maximum of 7-d average DMT; and the number of days on which maximum temperature exceeded 18, 20, or 22°C. We used Kolmogorov–Smirnov tests for continuous data to test for significant differences in streamflow (among seasons within the main stem) and temperatures (between sites and among seasons).

Our first objective was to quantify trout movements and assess differences in movement behaviors among seasons, between the main stem and tributary, and between brook trout and brown trout. Movement was quantified as the distance (m) between successive fish locations. We assigned positive values to upstream movements and negative values to downstream movements. We then constructed two-tailed frequency distributions of trout movement distance for each year. Our analyses of these distributions followed the advection–diffusion framework described by Turchin (1998) and Skalski and Gilliam (2000), where advection refers to the direction of movement (upstream versus downstream) and diffusion refers to variation in movement distance by individuals in the population (Petty and Grossman 2004).

Because movement distance was correlated with the number of days between resightings, we converted all measurements of movement to a movement rate (= [movement distance]/[number of days between successive sightings]). These data were then analyzed on a track-by-track basis by examining movement rates between successive sightings. We also analyzed the data on the basis of overall movement rates of each individual fish over the course of the study. Specifically, we calculated the total net movement rate (including upstream and downstream movements) and the total absolute movement rate for each fish in each season. We used *t*-tests to evaluate the null hypothesis that overall net displacement by trout did not differ significantly from zero. Rejection of this hypothesis would suggest a directional tendency (i.e., upstream versus downstream) in trout movements. We tested for differences in movement rates among seasons, between years, between streams, and between species by conducting either *t*-tests or analyses of variance on log-transformed movement rates.

Our second objective was to correlate trout movements with variation in water temperature and access to coldwater areas. We examined the effects of daily variation in temperature, flow, and access to known coldwater sources on trout movements during summer months. These analyses employed simple and multiple linear regressions in which the dependent variable was the log-transformed movement rate of fish on a track-to-track basis. Independent variables included the maximum ambient water temperature between successive sightings, the 7-d average DMT, maximum stream discharge between sightings, and the distance (m) between the fish and a known coldwater source prior to the movement occurring. Through extensive observations in the upper Shavers Fork watershed, we identified nine distinct coldwater sources within the study reaches of the Shavers Fork main stem.

Our third objective was to assess whether changing thermal conditions influenced microhabitat use by brook trout residing in the Shavers Fork main stem. Ambient water temperature was derived from continuous temperature loggers that were deployed throughout the study area. Focal water temperature was measured at the time of each fish observation. We then calculated the temperature difference by subtracting ambient temperature from the focal temperature. Positive values indicated conditions where individual trout inhabited microhabitats with warmer-than-ambient temperatures, whereas negative values indicated that fish inhabited cooler-than-ambient temperatures.

Because trout residing in the main stem exhibited a shift in temperature selection behaviors depending on ambient water temperature, we divided all main-stem observations into one of three temperature groups for further analyses. Temperature groups were determined based on the relationship between temperature differences, recorded ambient temperature, and documented behavioral thresholds of trout. Group 1 represented instances in which individuals inhabited microhabitats with focal point temperatures that were approximately equal to ambient (i.e., within $\pm 1^\circ\text{C}$) and where ambient temperature was ideal (13–17°C). Group 2 represented instances in which microhabitat use equaled ambient temperature, but ambient temperature was relatively warm (17–24°C). Group 3 included observations of trout inhabiting microhabitats that were notably cooler than the ambient temperature ($>2^\circ\text{C}$ cooler) when ambient temperatures were warm (17–24°C). We then used chi-square (χ^2) analysis to test for significant differences in microhabitat use among the different temperature groups. These analyses were used to test the null hypothesis of no significant effect of thermal conditions on microhabitat use by trout residing in the main stem.

RESULTS

Water Temperature and Flow

Average flow conditions in Shavers Fork were significantly lower in fall 2000 than in summer 2000 (Kolmogorov–Smirnov

TABLE 2. Summary statistics describing water temperature and streamflow in the main-stem Shavers Fork and its tributary, Rocky Run, during summer (SU; June 5–August 15) and fall (FA; September 5–November 15) study periods (DMT = daily maximum temperature; ND = no data).

Variable	Rocky Run			Shavers Fork		
	SU 2000	FA 2000	SU 2001	SU 2000	FA 2000	SU 2001
Average DMT (°C)	14.9	9.9	15.2	19.0	12.3	19.2
Maximum recorded ambient temperature (°C)	18.3	15.7	18.7	23.3	20.3	24.4
Average 7-d average DMT (°C)	15.1	10.0	15.3	19.1	12.4	19.3
Maximum 7-d average DMT (°C)	17.8	15.1	18.2	21.8	18.2	23.0
Number of days on which maximum temperature > 18°C	4	0	5	51	5	48
Number of days on which maximum temperature > 20°C	0	0	0	24	1	30
Number of days on which maximum temperature > 22°C	0	0	0	6	0	10
Mean daily flow (m ³ /s)	ND	ND	ND	2.72	2.39	3.12

test statistic $D = 0.03$, $n = 214$, $P < 0.05$); however, streamflows were relatively consistent for summer 2000 and summer 2001 (Table 2). As expected, water temperature was consistently lower in Rocky Run than in the Shavers Fork main stem (Table 2; Figure 2). Water temperatures in Rocky Run never exceeded 19°C, and in only a few cases did temperatures exceed 18°C. In contrast, water temperatures in the Shavers Fork main stem consistently exceeded 20°C during the summer study periods (Table 2; Figure 2). Values for the maximum 7-d average DMT peaked at 21.8°C in 2000 and 23.0°C in 2001. Although temperature patterns did not differ significantly between summer 2000 and summer 2001, overall cooler conditions were observed in summer 2000 (only 6 d with a maximum temperature > 22°C) than in summer 2001 (10 d with a maximum temperature > 22°C; Table 2; Figure 2).

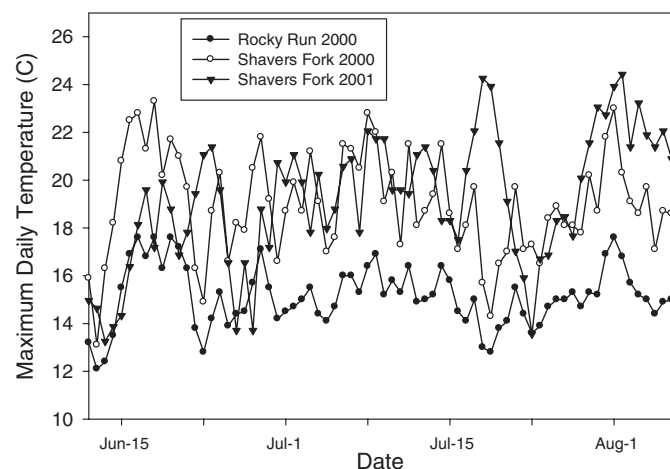


FIGURE 2. Year-to-year variation in the daily maximum water temperature (°C) measured in the Shavers Fork main stem and Rocky Run. Data are from the summer sampling periods (June 5–August 15) in 2000 and 2001. Rocky Run thermal regimes are relatively stable from year to year; consequently, only 2000 data are shown.

Trout Movement

We implanted transmitters into 84 trout and monitored the fish between June 5 and August 15 in 2000 and 2001 and between September 5 and November 15 in 2000. Days at large for individual fish ranged from 8 to 71 d, and the number of locations per individual trout ranged from 2 to 11. To avoid bias in the movement data set, we included only individuals that were located on four or more occasions. Three brook trout were returned by anglers after the study was completed. Three additional trout (2 brown trout, 1 brook trout) were found dead over the course of the entire study; those fish apparently died from surgical complications or predation. Six trout (3 brown trout, 3 brook trout) were released but were never recorded again during the entire study.

Brook trout residing in Rocky Run did not exhibit significant directional movements during the summer tracking season ($t = 0.97$, $P = 0.36$) or fall tracking season ($t = 1.45$, $P = 0.17$; net dispersal rate in Table 3). This was also true for brook trout ($t = 1.33$, $P = 0.41$) and brown trout ($t = 1.53$, $P = 0.16$) in the Shavers Fork main stem during fall 2000. However, brook trout and brown trout exhibited significant upstream movement tendencies (net dispersal rate > 0) in the main stem during summer months (Table 3). For example, brook trout moved an average distance of 2.3 km upstream in summer 2000 ($t = 5.6$, $P = 0.001$) and 1.2 km in summer 2001 ($t = 4.12$, $P = 0.001$). Likewise, the average distance moved by brown trout was 0.8 km upstream in summer 2001 ($t = 4.19$, $P = 0.004$; Table 3).

The movement rates of brook trout residing in Rocky Run were relatively low during the summer and fall tracking seasons (Table 3; Figure 3). Total dispersal rates in summer 2000 ranged from 1 to 8 m/d, with a mean of 3.3 m/d and a median of 2.1 m/d (Table 3). Mean dispersal rates of Rocky Run brook trout were slightly higher in fall 2000 (5.6 m/d), but this increase was driven by one highly mobile individual, which moved 2 km over the course of the fall 2000 tracking season (Table 3). Consequently, we did not observe significant seasonal variation in movement rates of brook trout inhabiting Rocky Run ($F = 1.1$; $df = 2, 28$; $P = 0.34$).

TABLE 3. Brook trout and brown trout movement in the main-stem upper Shavers Fork and its tributary, Rocky Run, during summer 2000, fall 2000, and summer 2001 (min = minimum value; max = maximum value). Net dispersal considers movements upstream and downstream. Total dispersal is the absolute value of movement distance. Days at large are the total number of days for which an individual was known to be present in the study area.

Variable	N	Mean	SE	Median	Min	Max
Brook Trout in Rocky Run, Summer 2000						
Net dispersal (m)	9	41	37	32	-154	272
Net dispersal rate (m/d)	9	1.0	1.0	0.6	-3.9	7.6
Total dispersal (m)	9	133	30.4	76.0	39.0	278.0
Total dispersal rate (m/d)	9	3.3	1.0	2.1	1.0	7.7
Days at large	9	42	4.0	40	23	65
Brook Trout in Shavers Fork, Summer 2000						
Net dispersal (m)	14	2,318	458	2,122	31	6,489
Net dispersal rate (m/d)	14	62	11	57	0.6	143
Total dispersal (m)	14	2,362	449	2,142	219	6,515
Total dispersal rate (m/d)	14	63	11	58	6	143
Days at large	14	38	2.8	38	20	61
Brook Trout in Rocky Run, Fall 2000						
Net dispersal (m)	16	194	129	3.0	-2.0	2,000
Net dispersal rate (m/d)	16	5.4	3.7	0.1	-0.1	58.8
Total dispersal (m)	16	202	129	5.0	1.0	2,000
Total dispersal rate (m/d)	16	5.6	3.7	0.1	0	58.8
Days at large	16	38	2	38	26	52.0
Brook Trout in Shavers Fork, Fall 2000						
Net dispersal (m)	2	4.0	3.0	4.0	1.0	7.0
Net dispersal rate (m/d)	2	0.1	0.1	0.1	0.01	0.2
Total dispersal (m)	2	21	12	21	9.0	33
Total dispersal rate (m/d)	2	0.4	0.2	0.4	0.2	0.6
Days at large	2	47	7	47	40	54
Brown Trout in Shavers Fork, Fall 2000						
Net dispersal (m)	10	4.9	2.7	4.5	-6.0	21.0
Net dispersal rate (m/d)	10	0.1	0.1	0.1	-0.2	0.6
Total dispersal (m)	10	10.1	2.0	9.5	0.0	21.0
Total dispersal rate (m/d)	10	0.3	0.1	0.3	0.0	0.6
Days at large	10	37	3	34	24	54
Brook Trout in Rocky Run, Summer 2001						
Net dispersal (m)	4	158	106	58	39	478
Net dispersal rate (m/d)	4	3.2	1.6	1.8	1.0	8.0
Total dispersal (m)	4	175	121	62	39	538
Total dispersal rate (m/d)	4	3.5	1.9	2.0	1.0	9.0
Days at large	4	41	7	38	28	60
Brook Trout in Shavers Fork, Summer 2001						
Net dispersal (m)	13	1,226	308	1,273	-254	2,780
Net dispersal rate (m/d)	13	26.6	6.4	28.1	-5.5	57.9
Total dispersal (m)	13	1,723	342	1,856	84	3,654
Total dispersal rate (m/d)	13	39.0	7.3	40.3	1.5	76.7
Days at large	13	45	3.0	46	20	64
Brown Trout in Shavers Fork, Summer 2001						
Net dispersal (m)	8	808	233	798	-5.0	2,051
Net dispersal rate (m/d)	8	18.9	4.5	20.4	-0.1	36.6
Total dispersal (m)	8	1,274	345	1,119	13.0	2,688
Total dispersal rate (m/d)	8	29.8	8.06	25.5	0.4	74.7
Days at large	8	42	3.9	44	20	56

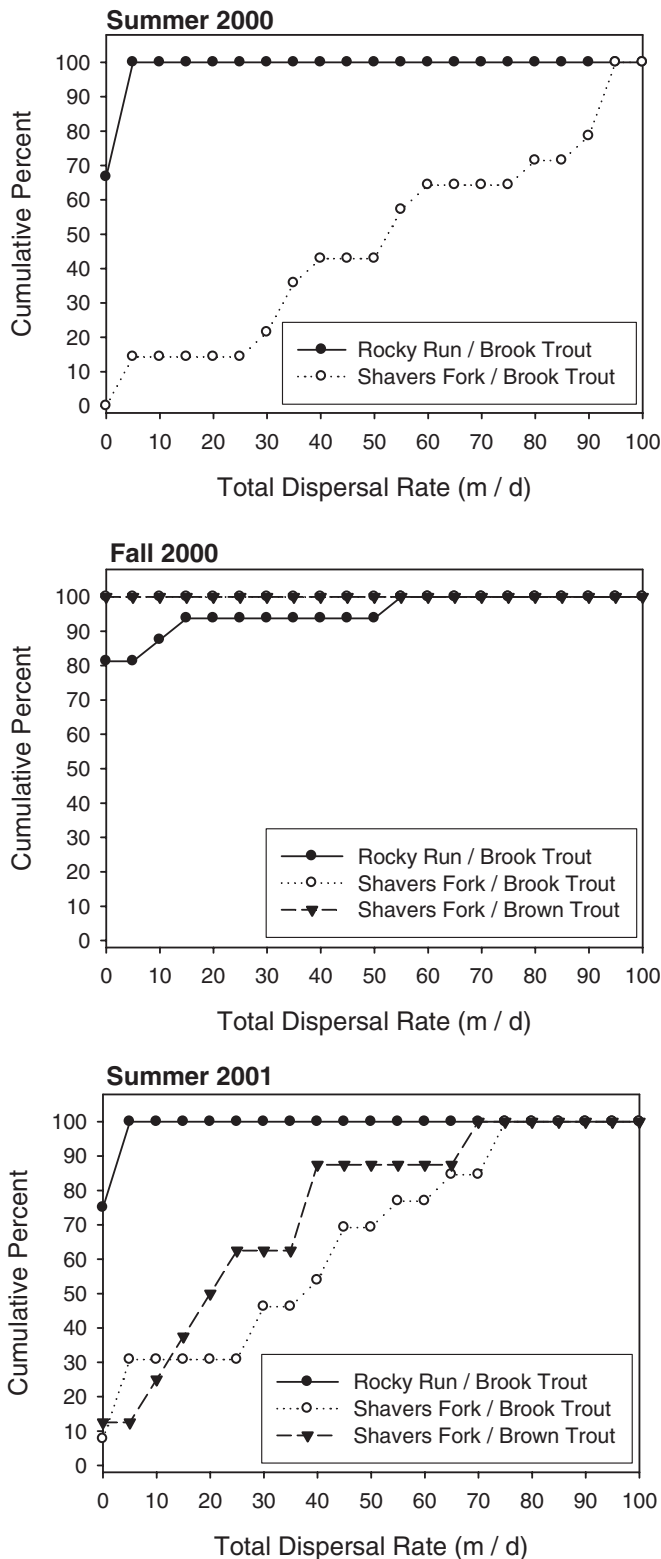


FIGURE 3. Cumulative frequency of movement rates (m/d) by brook trout and brown trout inhabiting Rocky Run and the Shavers Fork main stem. Total dispersal rate was calculated as the distance moved (regardless of direction) by individual trout divided by the number of days at large. Sample sizes for each season \times stream \times species combination are presented in Table 3.

In contrast, brook trout and brown trout inhabiting the Shavers Fork main stem exhibited high rates of dispersal during summer months (Table 3; Figure 3). Total dispersal rates of brook trout in summer 2000 ranged from 6 to 143 m/d (mean = 63 m/d; median = 58 m/d), and the maximum total displacement was 6.5 km. Overall rates of brook trout dispersal in the main stem dropped slightly in summer 2001, but this decline was not significant. Similarly, brown trout dispersal rates in summer 2001 ranged from 0.5 to 74.7 m/d, with a mean of 29.8 m/d and a median of 24.4 m/d. Movement rates in summer 2001 did not differ significantly between brook trout and brown trout ($F = 0.4$; $df = 1, 20$; $P = 0.54$). However, main-stem brook trout dispersal rates were significantly greater than tributary dispersal rates in summer 2000 and summer 2001 (2000: $F = 58.2$, $df = 1, 22$, $P = 0.001$; 2001: $F = 13.0$, $df = 1, 16$, $P = 0.003$; Table 3).

Trout dispersal rates declined dramatically during fall 2000 in the Shavers Fork main stem (Table 3; Figure 3). Total dispersal rates of brook trout in fall 2000 ranged from 0.2 to 0.6 m/d, with a mean and median of 0.4 m/d (estimates were based only on the movements of two individuals; Table 3). A similar decline in movement rates during fall 2000 was observed for brown trout as well (Table 3; Figure 3), with total dispersal rates ranging from 0.0 to 0.6 m/d. As a result, we observed a significant overall effect of season on the movement rates of brook trout ($F = 12.1$; $df = 2, 28$; $P = 0.002$) and brown trout ($F = 53.1$; $df = 1, 17$; $P = 0.0001$). However, we observed no significant difference in movement rates between brook trout and brown trout in either fall 2000 ($F = 0.8$; $df = 1, 11$; $P = 0.40$) or summer 2001 ($F = 0.4$; $df = 1, 20$; $P = 0.54$; Table 3).

Given the high rates of overall movement by brook trout in the Shavers Fork main stem, we examined the effects of temperature, streamflow, and distance to coldwater sources on brook trout movement during summer months. Brook trout movement rates were significantly related to maximum water temperature in summer 2000 and summer 2001. In summer 2000, movement rates decreased significantly as maximum temperature increased from 12°C to 18°C (Figure 4). In contrast, movement rates tended to increase as a function of maximum temperature when temperatures exceeded 18°C (Figure 4). In addition, multiple regression analyses indicated that maximum water temperature and distance to the nearest upstream coldwater source interacted to influence brook trout movement rates. During periods when ambient water temperatures exceeded 18°C, brook trout movement rates increased significantly with increasing maximum water temperature and with increasing distance to the nearest coldwater source ($F = 4.7$, $P = 0.001$, $R^2 = 0.26$). Ultimately, this led to an accumulation of brook trout at coldwater sources over the course of the summer, followed by a decrease in movement rates.

Trout Microhabitat Use

Brook trout and brown trout consistently used a subset of available microhabitats, regardless of season or stream (i.e.,

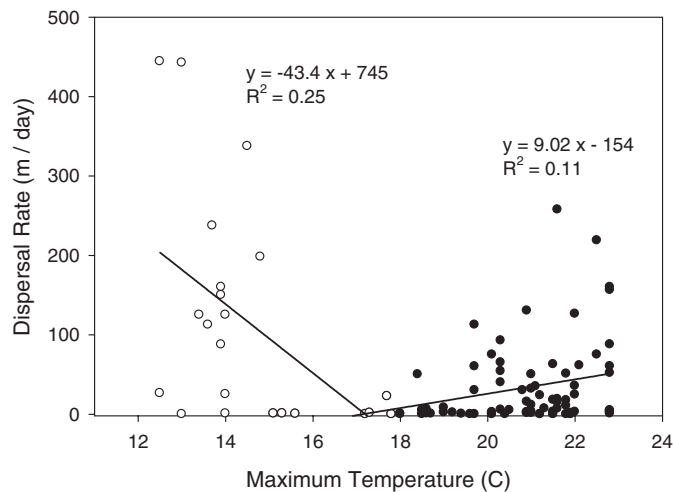


FIGURE 4. Relationship between brook trout movement rate (m/d) and the maximum ambient water temperature ($^{\circ}\text{C}$) in the Shavers Fork main stem during summer 2000. Open circles represent patterns during “cool” periods (i.e., maximum temperature $< 18^{\circ}\text{C}$). Black circles represent patterns during “warm” periods (i.e., maximum temperature $> 18^{\circ}\text{C}$).

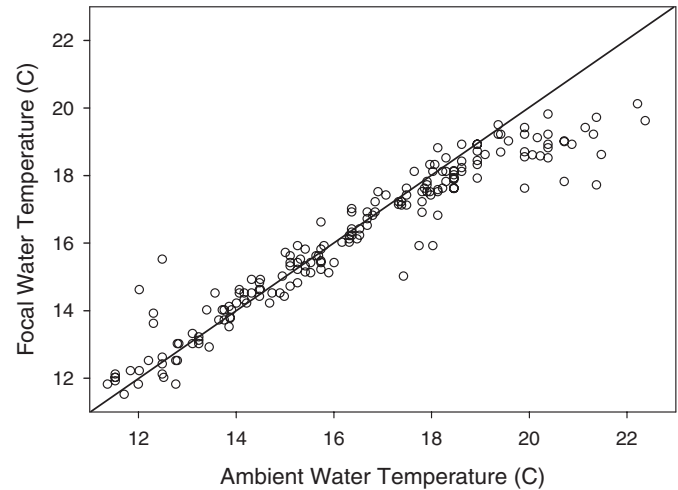


FIGURE 5. Relationship between focal point water temperature ($^{\circ}\text{C}$) for brook trout and brown trout and ambient water temperature in the Shavers Fork main stem and Rocky Run during summer 2000, fall 2000, and summer 2001. The dashed line represents the 1:1 relationship that would be expected if trout are selecting thermal microhabitats similar to ambient water temperature.

Shavers Fork main stem versus Rocky Run; Table 4). Trout were overrepresented in deeper microhabitats that had moderate to high average current velocities and that were close to cover (Table 4). An analysis of water temperatures at the focal position of trout in comparison with nearby ambient water temperatures revealed several important patterns (Figure 5). During the summer months, focal point temperatures never exceeded 20°C despite frequent periods in which ambient temperatures exceeded this threshold. In addition, we occasionally observed trout selecting slightly warmer-than-ambient water temperatures when ambient levels dropped below 13°C . Between 13°C and 17°C ,

however, focal point temperatures were always within $1\text{--}2^{\circ}\text{C}$ of ambient temperature (Figure 5).

Given the relationships observed in Figure 5, we calculated the focal point temperature difference as the focal point temperature minus the nearby ambient temperature. We then identified two ambient water temperature zones (ideal: $13\text{--}17^{\circ}\text{C}$; warm: $17\text{--}24^{\circ}\text{C}$) within which we observed different behavioral responses by trout (focal point temperature difference of $\pm 1^{\circ}\text{C}$ or $> 2^{\circ}\text{C}$). We then used χ^2 analysis to test the hypothesis that changing water temperatures would influence the types of physical microhabitats used by trout residing in the Shavers

TABLE 4. Mean (SE in parentheses) habitat availability and use by brook trout and brown trout in Rocky Run and Shavers Fork during all seasons. Brown trout were not sampled during summer 2000 (ACV = average current velocity; FCV = focal point current velocity; MCV = maximum current velocity within 1 m; DTC = distance to cover; B = boulder; W = wood; B/W = combination of boulder and wood; NA = not applicable).

Variable	Survey	Depth (cm)	ACV (cm/s)	FCV (cm/s)	MCV (cm/s)	DTC (m)	Cover type (% B, W, and B/W)
Rocky Run							
Availability		11 (0.9)	15 (1.3)	NA	NA	1.0 (0.7)	65, 23, 12
Brook trout use	Summer 2000	15 (0.8)	19 (1.6)	16 (1.2)	38 (1.5)	1.8 (0.3)	79, 18, 3
Brook trout use	Fall 2000	17 (0.4)	23 (0.6)	19 (0.4)	29 (0.4)	0.8 (0.06)	80, 8, 12
Brook trout use	Summer 2001	18 (0.9)	26 (1.0)	23 (1.0)	36 (1.2)	0.3 (0.1)	67, 5, 28
Shavers Fork							
Availability		17 (0.6)	22 (0.7)	NA	NA	2.0 (0.1)	82, 12, 6
Brook trout use	Summer 2000	23 (1.1)	25 (1.2)	21 (0.9)	39 (1.5)	4.5 (0.4)	86, 9, 5
Brook trout use	Fall 2000	20 (0.6)	25 (1.1)	20 (0.9)	31 (1.5)	0.6 (0.3)	100, 0, 0
Brook trout use	Summer 2001	22 (0.7)	26 (0.8)	24 (0.9)	36 (0.8)	0.5 (0.1)	79, 6, 15
Brown trout use	Fall 2000	19 (0.6)	24 (0.7)	19 (0.7)	30 (0.8)	1.0 (0.2)	100, 0, 0
Brown trout use	Summer 2001	23 (1.2)	24 (1.2)	20 (1.11)	35 (1.11)	0.6 (0.1)	90, 0, 10

TABLE 5. Mean (SE in parentheses) microhabitat characteristics and results of χ^2 analysis for three temperature group divisions of main-stem brook trout in summer 2000 and 2001. Temperature groups are (1) trout with a focal temperature difference of $\pm 1^\circ\text{C}$ and an ideal ambient water temperature; (2) trout with a focal temperature difference of $\pm 1^\circ\text{C}$ and a warm ambient water temperature; and (3) trout with a focal temperature difference greater than 2°C and a warm ambient water temperature (ACV = average current velocity; FCV = focal point current velocity; MCV = maximum current velocity within 1 m; DTC = distance to cover; ** $P < 0.01$).

Temperature group or statistic	Sample size	Depth (cm)	ACV (cm/s)	FCV (cm/s)	MCV (cm/s)	DTC (m)
1	85	22.4 (0.9)	26.6 (1.1)	21.9 (0.8)	38.9 (1.3)	3.2 (0.4)
2	55	21.4 (1.3)	25.8 (1.4)	20.7 (1.2)	37.3 (1.6)	2.0 (0.4)
3	25	20.3 (2.0)	24.3 (1.7)	19.9 (1.6)	34.4 (2.0)	1.6 (0.4)
χ^2		5.4	2.5	9.5	5.1	24.8**
df		8	6	6	8	6

Fork main stem. We tested for differences in microhabitat use among three groups of observations: group 1 consisted of trout with a focal temperature difference of $\pm 1^\circ\text{C}$ and an ideal ambient water temperature; group 2 consisted of trout with a focal temperature difference of $\pm 1^\circ\text{C}$ and a warm ambient water temperature; and group 3 consisted of trout with a focal temperature difference greater than 2°C and a warm ambient water temperature. Results from these comparisons showed similar use among groups in all microhabitat variables except distance to cover (Table 5). Trout in groups 2 and 3 (i.e., observed during periods of warm ambient conditions) tended to remain closer to cover than those in group 1 (Table 5).

DISCUSSION

Movement represents an important life history feature of many stream fishes, and numerous factors have been shown to influence whether fish adopt a mobile strategy. For example, spawning-related migrations are characteristic of many anadromous and land-locked salmonids. However, nonreproductive factors also influence fish mobility (Hughes 1998; Poff and Huryn 1998; Gilliam and Fraser 2001; Gowan and Fausch 2002; Hilderbrand and Kershner 2004; Olsson et al. 2006; Petty and Grossman 2010). Density-dependent interactions and competition for high-quality foraging habitats have been shown to influence fishes as different as Arctic grayling *Thymallus arcticus* (Hughes 1998) and mottled sculpin (Petty and Grossman 2010). Furthermore, biological processes (e.g., predation risk) may interact with physical processes (e.g., streamflow) to affect fish movement decisions (Gilliam and Fraser 2001). Regardless of the mechanism, a fish's ability to move between habitat patches that may be separated by a few meters or several kilometers allows for the individual's success on a riverscape scale that is unique to each species (Fausch et al. 2002). The purpose of our current study was to quantify the scale of brook trout and brown trout mobility and the relative importance of water temperature in affecting trout movement behaviors.

The first major finding from our study was that the relative mobility of brook trout within the upper Shavers Fork watershed

varied significantly depending on whether individuals resided within the larger main stem or the smaller tributary. On average, trout inhabiting the main stem during summer months exhibited a movement rate (50 m/d) that was an order of magnitude higher than that of tributary fish (2 m/d). This pattern was likely driven, in part, by differences in stream temperature between main-stem Shavers Fork and Rocky Run. Overall, water temperatures in the main stem were considerably warmer and much more variable than those recorded in the tributary. During the early summer, while water temperatures in the main stem ranged between 14°C and 17°C , trout moved at a relatively low rate in both the main stem and Rocky Run, indicating that this temperature range may be ideal for trout habitat selection. However, as the summer progressed and main-stem water temperatures warmed, trout in the main stem became increasingly mobile, whereas tributary trout remained relatively sedentary. Since the upper lethal temperature for brook trout is around 25°C (Taniguchi et al. 1998), it is not surprising that trout mobility increased as temperatures increased from 18°C to 25°C . In the tributary, water temperature never exceeded 19°C and only on a few occasions did it surpass 18°C .

Similar patterns of increased movement and the use of thermal refugia when ambient temperatures are outside of an optimal bioenergetic range have been observed in brown trout (Young et al. 2010), adult Chinook salmon *O. tshawytscha* (Gonia et al. 2006), and adult steelhead (anadromous rainbow trout; Keefer et al. 2009). Many studies have shown that brook trout and other salmonids use coldwater sources, such as tributaries, seeps, and groundwater upwellings, to avoid thermal (both upper and lower) stress (Baird and Krueger 2003; Gonia et al. 2006; Breau et al. 2007; Young et al. 2010). During the early summer, trout in the main stem also showed a higher affinity for movement when temperatures were much lower than 14°C . This further demonstrates the importance of stream temperature for influencing trout behavior and selection of optimal habitat in the upper Shavers Fork watershed.

Additional evidence suggests, however, that temperature alone cannot explain differences in the mobility of trout residing in the main-stem Shavers Fork and Rocky Run. When

temperatures were similar between the main stem and the tributary (e.g., during early summer and fall), trout movement was still more extensive in the main stem (although differences in movement were less distinctive). One potential explanation for this discrepancy is the presence of a mobile subpopulation residing in the main stem as opposed to a more sedentary population in the tributary. Petty et al. (2005) demonstrated that brook trout populations in larger streams of the upper Shavers Fork watershed are characterized by high rates of immigration and emigration, whereas populations in smaller tributaries have a relatively low turnover rate. These patterns are consistent with mobile versus sedentary subpopulations residing within main-stem and tributary habitats, respectively (Rodríguez 2002; Skalski and Gilliam 2000). Likewise, Martin (2010) demonstrated that transient brook trout were first to recolonize defaunated headwater streams. However, over time, brook trout populations in headwater streams became dominated by sedentary individuals. Martin (2010) reasoned that this "succession" of colonizers was likely due to the fact that the regional brook trout population consisted of a mixture of resident and mobile individuals.

Many previous studies have acknowledged likely divisions in mobility within populations of different salmonid species (Hilderbrand and Kershner 2004; Olsson et al. 2006; Utz and Hartman 2006; Stolarski and Hartman 2010) as well as other fishes (Skalski and Gilliam 2000; Schaefer et al. 2003; Petty and Grossman 2004; Hudy and Shiflet 2009). Different movement strategies involve different cost-benefit tradeoffs. For example, bioenergetic tradeoffs may occur when mobility enables access to productive foraging habitats but at the cost of higher predation risk, greater energy expenditure, or both. In contrast, resident fish would enjoy lower energetic costs in movement between habitat patches but may be restricted by the productivity of the local prey base and strong density dependence (Morinville and Rasmussen 2003; Hilderbrand and Kershner 2004; Grossman et al. 2010). Whether different movement strategies exhibited by individuals within a population represent permanent strategies or are variable from individual to individual over time (Petty and Grossman 2004) will be an important question for future studies of Appalachian brook trout.

Differences in movement among brook trout subpopulations in Shavers Fork may also be explained by competitive interactions. Intuitively, larger fish should be competitively dominant and should be able to maintain and defend the most energetically beneficial microhabitat available (Kristensen and Closs 2008), which may often lead to relatively low rates of mobility. However, other studies have indicated that fish become more mobile as body size increases (Petty and Grossman 2004, 2010; Sundt-Hansen et al. 2009). Petty and Grossman (2010) found that larger mottled sculpin were more likely to leave established foraging territories than smaller individuals when the same quantity of prey was available. They reasoned that this was due to competitively dominant mottled sculpin being able to win most disputes over preferred habitat patches, and consequently the larger fish

could find and gain access to the best foraging microhabitats in the riverscape (Petty and Grossman 2010). The tendency for larger fishes to display movement may also be associated with seasonal variability. Gowan and Fausch (2002) argued that temporal shifts in habitat quality (i.e., quality in foraging patches) likely influence larger, dominant fish to move between habitat patches in order to continually utilize the highest quality habitat patches available. Individual fish must be mobile and must be ready to act on changing instream conditions to ensure optimal growth and survival (Dolloff and Flebbe 1994; Gowan and Fausch 2002; Young et al. 2010). Some reaches utilized by trout in the Shavers Fork main stem during early summer, for example, were not inhabited by trout during the late summer. These shifts in mobility were likely related to changes in ambient water temperature and are indicative of individual habitat selection decisions that enable competitively dominant trout to avoid thermal extremes and maximize access to the highest quality habitats in the riverscape (Gowan and Fausch 2002; Petty and Grossman 2010).

A second important pattern observed in this study was the significance of microhabitat selection by brook trout as a means of thermoregulation. Prior to this study, we expected that brook trout residing in the Shavers Fork main stem would disperse into colder tributaries during the summer as main-stem temperatures increased from ideal conditions to highly stressful conditions. However, brook trout did not abandon the main stem but instead selected main-stem microhabitats that provided thermal refugia. Access to coldwater seeps, tributary confluences, and groundwater upwellings was particularly important when summer stream temperatures reached stressful levels for brook trout. As ambient stream temperatures increased, microhabitat characteristics such as distance to coldwater sources and distance to cover were among the dominant factors that predicted the presence of trout.

Microhabitats with cold water and cover are important not only because they relieve thermal stress but may also provide highly productive habitat for prey species. In the main stem, tributary confluences have been shown to contain higher densities of coarse substrate and LWD (Benda et al. 2004; Kiffney et al. 2006), which are known to support high invertebrate productivity (Benke et al. 1985). The cooler water from the tributary, pool formation by LWD, and higher productivity of invertebrate prey species at these main-stem-tributary confluences provide ideal bioenergetic characteristics for brook trout production. Hartman and Logan (2010) found that brook trout strongly selected for pool habitats with LWD; they attributed these findings to the importance of LWD in creating pool habitat as well as in supporting prey production through accumulation of organic matter. Selection of pool habitat close to cover (like LWD) was also consistent in our study (especially near confluences) and is likely important for providing refuge from harsh thermal conditions as well as for allowing exploitation of highly productive main-stem foraging sites (Petty et al. 2005).

A major limitation to this study was that we were restricted by the transmitter weight : body weight ratio (Winter 1983) and could only study large, adult trout for relatively short periods of time. Juvenile trout are known to be more sensitive to temperature and therefore may be more important for use in establishing temperature criteria for restoration efforts (Selong et al. 2001). A greater number of individuals tagged and followed throughout multiple areas of the watershed would greatly strengthen our study. In addition, study periods that incorporate a greater temporal scale would be beneficial. For example, we know that during the fall, brook trout move from the main stem into tributaries to spawn. However, the timing of brook trout returns to the main stem remains unknown.

Conclusions and Management Implications

The results of our study indicate that brook trout residing in larger river main stems exhibit considerably higher rates of movement than trout residing in smaller tributaries. Our study further suggests that water temperature and the need to access thermal refugia are the predominant mechanisms controlling the movement behaviors of main-stem trout. Finally, our results are consistent with the hypothesis that the overall brook trout population comprises a sedentary fraction that remains within the tributaries year-round and a mobile fraction that utilizes the highly variable but productive main stem as foraging habitat (Petty et al. 2005). Movement should be viewed as an adapted behavior used by large adult trout in the Shavers Fork to adjust to spatially and temporally varying habitat conditions and to reach complementary and supplementary habitat distributed at a watershed scale (Fausch et al. 2002; Gowan and Fausch 2002; Petty et al. 2005; Young et al. 2010). Our findings are in agreement with Gowan et al. (1994), who stated that movement may be more common in variable or harsh systems (e.g., the main stem) and less common in more constant habitats (e.g., small tributaries).

Brook trout conservation within larger main stems such as the Shavers Fork will require protection of existing coldwater sources and creation of new coldwater sources (e.g., cold tributary inflows, hyporheic upwelling, deep pools that intercept the water table, and lateral groundwater seeps), especially in the face of climate change (Flebbe et al. 2006). For example, riparian management and canopy re-establishment (Carline and Walsh 2007) in upper reaches of the Shavers Fork main stem would likely have beneficial effects on water temperature and trout populations downstream. In addition, channel habitat enhancement projects that focus on pool formation and creation of coldwater microhabitats within the main stem could reduce thermal stress and the need for energetically costly long-range movements by trout (Torgersen et al. 1999). Improving habitat heterogeneity and access to thermal refugia within the main stem would likely benefit brook trout populations within the entire watershed. Trout would be able to exploit highly productive main-stem habitats with less thermal stress and would also expe-

rience reduced isolation among tributaries where reproduction occurs (Petty et al. 2005).

Finally, evidence of a mobile fraction within the upper Shavers Fork brook trout population emphasizes the need for management actions that protect mobile individuals and facilitate their movement within the watershed. As we have seen, high rates of movement by trout are needed to link high-quality reproductive habitats in the headwaters with highly productive foraging habitats in the main stem (Petty et al. 2005). Furthermore, trout require mobility to respond to catastrophic events that may result in streamwide extirpation of populations (Roghair and Dolloff 2005). However, mobile brook trout may be highly susceptible to angler harvest (Johnston and Post 2009) and isolation below dispersal barriers (Poplar-Jeffers et al. 2009). Consequently, maximizing brook trout productivity at the whole-watershed scale may be achieved only through integrated efforts to provide thermal refugia in the main stem, remove dispersal barriers to enable movement between the main stem and tributaries, and protect mobile individuals from harvest through whole-watershed catch-and-release regulations.

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