

Spatial and temporal movement dynamics of brook *Salvelinus fontinalis* and brown trout *Salmo trutta*

Lori A. Davis  · Tyler Wagner ·
Meredith L. Bartron

Received: 10 October 2014 / Accepted: 12 June 2015
© Springer Science+Business Media Dordrecht 2015

Abstract Native eastern brook trout *Salvelinus fontinalis* and naturalized brown trout *Salmo trutta* occur sympatrically in many streams across the brook trout's native range in the eastern United States. Understanding within- among-species variability in movement,

Electronic supplementary material The online version of this article (doi:10.1007/s10641-015-0428-y) contains supplementary material, which is available to authorized users.

Disclaimer: This draft manuscript is distributed solely for purposes of scientific peer review. Its content is deliberative and predecisional, so it must not be disclosed or released by reviewers. Because the manuscript has not yet been approved for publication by the US Geological Survey (USGS), it does not represent any official finding or policy.

L. A. Davis (✉)
Pennsylvania State University,
University Park, PA 16802, USA
e-mail: Lori_Davis@fws.gov; loriadavis78@gmail.com

T. Wagner
U.S. Geological Survey, Pennsylvania State University,
University Park, PA 16802, USA

M. L. Bartron
U.S. Fish and Wildlife Service, U.S. Fish and Wildlife
Service, Northeast Fishery Center,
Lamar, PA 16848, USA

Present Address:

L. A. Davis
U.S. Fish and Wildlife Service, Northeast Fishery Center,
Lamar PA, USA

including correlates of movement, has implications for management and conservation. We radio tracked 55 brook trout and 45 brown trout in five streams in a north-central Pennsylvania, USA watershed to quantify the movement of brook trout and brown trout during the fall and early winter to (1) evaluate the late-summer, early winter movement patterns of brook trout and brown trout, (2) determine correlates of movement and if movement patterns varied between brook trout and brown trout, and (3) evaluate genetic diversity of brook trout within and among study streams, and relate findings to telemetry-based observations of movement. Average total movement was greater for brown trout (mean \pm SD = 2,924 \pm 4,187 m) than for brook trout (mean \pm SD = 1,769 \pm 2,194 m). Although there was a large amount of among-fish variability in the movement of both species, the majority of movement coincided with the onset of the spawning season, and a threshold effect was detected between stream flow and movement: where movement increased abruptly for both species during positive flow events. Microsatellite analysis of brook trout revealed consistent findings to those found using radio-tracking, indicating a moderate to high degree of gene flow among brook trout populations. Seasonal movement patterns and the potential for relatively large movements of brook and brown trout highlight the importance of considering stream connectivity when restoring and protecting fish populations and their habitats.

Keywords Brook trout · Brown trout · Fish movement

Introduction

The eastern brook trout *Salvelinus fontinalis* is a cold-water salmonid with a native range in the eastern United States that extends along the Appalachians from Georgia to Maine. Populations are in decline throughout its native range as a result of a variety of factors that have resulted in the degradation of physical and chemical stream and riparian habitats. In addition, anthropogenic activities (e.g., agricultural activities and natural gas exploration) and climate change have the potential to continue to negatively affect brook trout habitat through direct effects of habitat loss and fragmentation resulting in decreased stream connectivity (Malmqvist and Rundle 2002; Stranko et al. 2008). In addition to physio-chemical habitat degradation, naturalized brown trout *Salmo trutta* have been identified as a threat to native brook trout populations (EBTJV 2011). In fact, studies have indicated a variety of negative effects of brown trout on wild brook trout populations (Fausch and White 1981; Waters 1983; Grant et al. 2002; Wagner et al. 2013a), largely as a result of brown trout's competitive superiority over brook trout.

Given the potential negative effects of brown trout, and future fragmentation of brook trout habitat due to land use and climate change (e.g., thermal fragmentation; (Eby et al. 2014)), a better understanding of brook and brown trout movement patterns is necessary. For example, this information may aid management agencies in evaluating the recolonization potential of brook trout in degraded stream reaches that are also accessible by brown trout. In addition, brown trout are an important ecological and economical game species in many areas, even where they are non-native. For example, brown trout were first introduced in Pennsylvania in the late 1800s and since their introduction they have become naturalized in Pennsylvania streams where they are widespread and the dominant trout species in many streams (Steiner 2000). Therefore, quantifying brown trout movements may aid in identifying habitat requirements necessary for this species to complete essential life history requirements. Thus, understanding movement dynamics can aid

resource management agencies identify conditions that might facilitate a species' persistence, establishment, and dispersal (DeGrandchamp et al. 2008), and ultimately increase adaptive potential (Sgrò et al. 2011). This is particularly important for coldwater fish species whose range is largely restricted by unsuitable water temperatures present in larger downstream streams (Ayllón et al. 2013).

Although quantifying movement of stream fishes using traditional tagging techniques, such as radio telemetry, provides information on short-term dynamics, they do not provide information about the demographic effects of dispersal that can maintain populations and increase population persistence. Movement by individuals can have demographic effects on the structure and size of populations affecting recruitment, persistence and extinction rates (Wilson et al. 2004; Kanno et al. 2014). As such, quantifying genetic diversity within and between streams in conjunction with traditional tagging methods can provide important insight into gene flow that may be occurring as a function of observed movement. Although gene flow over large geographic scales has been studied for some time, recent advances of highly variable markers (i.e., microsatellites) have facilitated the ability to examine population genetic structure at a finer scale (e.g., within-watershed). Salmonid population genetic structure on a microgeographical scale has been detected (Angers et al. 1995; Spruell et al. 1999), and therefore the use of microsatellite markers should provide some estimation of dispersal and movement at a local level. Thus, direct (tagging) methods coupled with indirect (microsatellite analysis) methods can provide an increased understanding of the movement dynamics among and within populations over both short-term and longer time scales. The overall objectives of this study were to (1) evaluate the late-summer, early winter movement patterns of brook trout and brown trout, (2) determine correlates of movement and if movement patterns varied between brook trout and brown trout, and (3) evaluate genetic diversity of brook trout within and among study streams, and relate findings to telemetry-based observations of movement. We focused genetic analysis on brook trout because it is a native species of concern in our study area and was present in all streams; whereas, brown trout are a naturalized species and were not present in all study streams.

Materials and methods

Study area

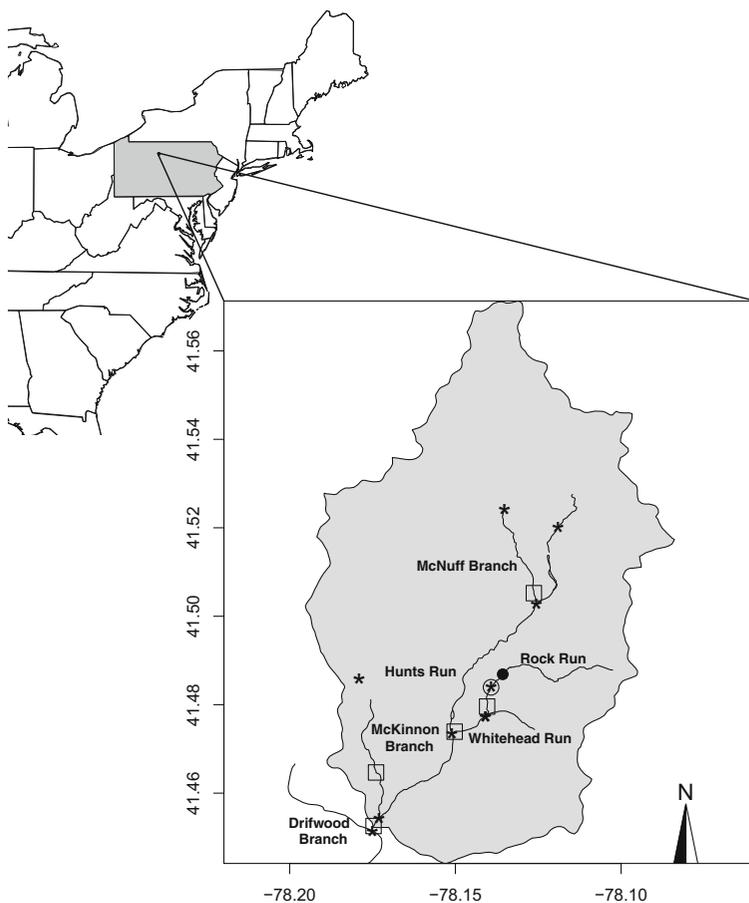
Study streams were located in north-central Pennsylvania, USA in the Hunts Run Watershed (Fig. 1). The Hunts Run Watershed is heavily forested with both deciduous hardwood and evergreen tree species and encompasses a 79.2 km² drainage area and is located primarily in Cameron County, PA. The study streams included the mainstem of Hunts Run and four tributaries that drain directly into Hunts Run: McKinnon Branch, McNuff Branch, Rock Run, and Whitehead Run (Fig. 1). Rock Run was the only allopatric brook trout stream. Hunts Run drains into a larger system known as the Driftwood Branch of Sinnemahoning Creek (hereafter referred to as Driftwood Branch). The only potential barrier to movement within the

watershed was a 2.5 m vertical waterfall located approximately 850 m upstream from the confluence of Rock Run with Whitehead Run (Fig. 1). Fish were not sampled upstream of this natural barrier as it was assumed to prevent any upstream movement by fish (Adams et al. 2000).

Surgical implementation of radio-transmitters

Between 13 September 2012 and 20 September 2012, 55 brook trout and 45 brown trout, were captured and surgically implanted with Lotek (Lotek Wireless Inc., Newmarket Ontario, Canada) NanoTag series digitally coded transmitters (NTC-3-2 1.1 g; 124 d life expectancy; active between 600 and 1800 hours.). This time of year was selected for tagging because it preceded the spawning time of both species for Pennsylvania streams (Wydoski and Cooper 1966). In

Fig. 1 Map of study streams located in the Hunts Run Watershed in north-central Pennsylvania, USA. Solid circle on Rock Run is the location of a waterfall that is the only known barrier to movement within the watershed. Open squares are locations of staff gages and 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)



addition, stream temperatures $> 18^{\circ}\text{C}$ limited the opportunity to implant radio transmitters earlier in the year. A crew worked upstream to capture trout using pulsed-DC electrofishing in Hunts Run (13 brook and 17 brown trout), McKinnon Branch (10 brook and 10 brown trout), McNuff Branch (8 brook and 12 brown trout), Whitehead Run (14 brook, and 6 brown trout) and Rock Run (10 brook trout; brown trout were not present in Rock Run). Brook trout weighed between 45 – 417 g (mean \pm SD, 102 ± 60) and measured 162 – 345 mm (214 ± 32). Brown trout captured weighed between 46 – 829 g (166 ± 158) and measured 161 – 430 mm (246 ± 49) in length. The shielded-needle technique was used for surgical implantation of transmitters (Ross and Kleiner 1982). Fish were anesthetized using tricaine methanesulfonate (MS-222) during surgery. All trout were presumed sexually mature and age-1 or older. However, a confident determination of sex could not be made for all fish. Fish were sampled throughout each stream reach in order to obtain an even distribution in stream distance between individuals. Fish were released into the stream within 50 m of their the point of capture.

Radio tracking

Tracking fish was performed by two crews of two persons, beginning on 16 September 2012. Either visual identification or signal strength was used to identify the location of each fish. Based on locating shed transmitters and transmitters from predated fish, as well as trials where crew members hid a transmitter, error of signal strength was estimated to be within 1 m^2 of the actual fish's location. Mollenhauer et al. (2013) found similar error estimates among radio-tagged brook trout in Pennsylvania. Once each fish was located, a GPS location, using a Trimble GeoXH 6000 centimeter edition (Trimble Navigation Inc., Sunnyville, CA) GPS unit, was logged. Using Trimble Terrasync (Trimble Navigation Inc., Sunnyville, CA) field software, coupled with Trimble Pathfinder (Trimble Navigation Inc., Sunnyville, CA) office software, locations were estimated to be within 0.1 centimeter GPS accuracy. For fish that moved into the Driftwood Branch, locations were primarily made by vehicle because of limited stream-side walking access. Specifically, researchers drove along a road that ran parallel to the Driftwood Branch to locate fish utilizing a radio-receiver.

Fish movement calculations

Longitudinal profiles were created for each of the five study streams: Hunts Run (11.7 km), McKinnon Branch (4.1 km), McNuff Branch (3.0 km), Whitehead Run (1.4 km), and Rock Run (847 m). This resulted in a total of approximately 21 km of stream reach surveyed (Fig. 1). Latitude and longitude were assigned to each elevation measurement of the thalweg profiles based on the linear distance between the GPS points logged. A digital map of the streams was then created that allowed for calculations of stream distance moved, rather than linear distance, between fish locations.

Movement between consecutive fish locations and total movement was calculated as distance moved (m) for each fish and was not based on direction (i.e., regardless of stream flow direction). Furthest upstream and furthest downstream movement was calculated as the furthest upstream and downstream distance, respectively, a fish was located from its initial location. In a few cases (for 8 fish), individuals moved in a downstream direction from the stream they were previously located in and then in an upstream direction into another stream. For these cases, movement was considered negative (e.g., downstream) because of the general downstream movement displayed. Fish were assigned to a specific study stream based on the stream they were last located and had spent more than half the number of days in the study.

Stream flow and water temperature

Stream flow and water temperature ($^{\circ}\text{C}$) were monitored throughout the study. Staff gages were installed in Hunts Run, McKinnon Branch, McNuff Branch, Rock Run and Whitehead Run (Fig. 1). The unauthorized removal of the Rock Run staff gage in October 2012 prevented measuring stream flow stage in Rock Run. After this date, stream flow measurements for Rock Run were presumed to be similar to Whitehead Run, as Rock Run provides almost 100 percent of the flow to Whitehead Run. HOBO ProV2 temperature loggers (Onset Computer Corporation, Bourne, MA, USA) were deployed in each study stream to measure water temperature every 30 minutes. The flow covariate used in modeling was the change in flow between consecutive fish locations and was based on daily observations of stream flow stage taken for each

stream. The temperature covariate was the change in maximum water temperature between consecutive fish locations.

Statistical modeling

To examine temporal dynamics in brook and brown trout movement, we fitted Bayesian dynamic linear models (DLM) (Wagner et al. 2013b). The DLM was parameterized as follows:

Observation equation:

$$y_{ti} = level_t + \psi_{ti}, \psi_{ti} \sim N(0, \Psi_t) \tag{1}$$

Systems equations:

$$level_t = level_{t-1} + rate_t + \omega_{t1}, \omega_{t1} \sim N(0, \Omega_{t1}) \tag{2}$$

$$rate_t = rate_{t-1} + \omega_{t2}, \omega_{t2} \sim N(0, \Omega_{t2}) \tag{3}$$

Where y_{ti} is log_e -transformed movement for fish i on day t . We added a constant of 1 m to accommodate observations of zero movement prior to log-transforming the data. The addition of 1 m implies that zero estimates for movement are not true zeros. This is a reasonable assumption given that it is highly unlikely that a fish never moved between relocations. $level_t$ is the mean log_e movement at time t ; $rate_t$ is the expected rate of change of movement (i.e., the slope between consecutive time periods); and ψ_{ti} and ω_{tj} ($j = 1,2$) are the error terms for day t , which are distributed as $N(0, \Psi_t)$ and $N(0, \Omega_{t1})$. Diffuse priors were used for all parameters (see Wagner et al. 2013b) for details). We fitted DLMS to time-series for both brook and brown trout combined and for each species separately to investigate differences in temporal dynamics. The models were estimated using Bayesian estimation and the program JAGS was used for all analyses (Plummer 2013), run within R (Core Team 2013). After discarding the first 10,000 samples, we retained every 3rd sample for a total of 60,000 samples. We examined the scale reduction factor, a convergence statistic, for each parameter, trace plots, and plots of posterior distributions to assess convergence.

We fitted hierarchical models to quantify the effects of covariates on movement. The general form of the model was:

$$y_i \sim N(\beta_0 + \alpha_{j(i)}^{fish}, \sigma_{j(i)}^2), \text{ for } i, \dots n \tag{4}$$

$$\alpha_j^{fish} \sim N(\alpha_{m(j)}^{stream}, \sigma_{fish}^2), \text{ for } j, \dots J \tag{5}$$

$$\alpha_m^{stream} \sim N(0, \sigma_{stream}^2), \text{ for } m, \dots M \tag{6}$$

$$log(\sigma_j) \sim N(\mu_\sigma, \omega_\sigma^2), \text{ for } j, \dots J \tag{7}$$

Where β_0 is a fixed intercept (the grand mean log_e movement), $\alpha_{j(i)}^{fish}$ is the fish-specific deviation from the grand mean in log_e movement, $\sigma_{j(i)}^2$ is the fish specific residual standard deviation, $\alpha_{m(j)}^{stream}$ is the stream-specific deviation in log_e movement, σ_{fish}^2 is the variation among fish in log_e movement, σ_{stream}^2 is the variation among streams in log_e movement, μ_σ is the grand-mean residual standard deviation, and ω_σ^2 is the variation among fish in residual standard deviation. Diffuse normal priors were used for β_0 and μ_σ . Diffuse uniform priors were used for σ_{fish} , σ_{stream} , and ω_σ .

Covariates can be added to any level of the model (e.g., observation, fish, or stream-level). For example, a dummy variable for the effect of species was added to investigate if brook and brown trout differed in average movement and if residual variability differed among species. Equations 2 and 4 were modified accordingly:

$$\alpha_j^{fish} \sim N(\alpha_{m(j)}^{stream} + \gamma_1^{\alpha fish} \times species_j, \sigma_{fish}^2), \text{ for } j, \dots J \tag{8}$$

$$log(\sigma_j) \sim N(\gamma_{1k(j)}^{\sigma fish}, \omega_\sigma^2), \text{ for } j, \dots J \text{ and } k = 1, 2 \tag{9}$$

Where $\gamma_1^{\alpha fish}$ is the effect of species, where $species_j$ was coded 1 if brown trout, 0 otherwise (effects parameterized), and where $\gamma_{1k(j)}^{\sigma fish}$ is the effect of species on residual standard deviations among fish (means parameterized).

Because we hypothesized an abrupt change in movement given covariates of flow and temperature, we modified Eq. 4 to fit a threshold model as follows:

$$y_i \sim N(\beta_0 + \beta_1 x_i + \delta(x_i - \phi)_+ \alpha_{j(i)}^{fish}, \sigma_{j(i)}^2), \text{ for } i, \dots n \tag{10}$$

Where movement was modeled as a function of a covariate x_i and where β_0 is the intercept and β_1 is the regression slope prior to the change point and δ is the change in regression slopes after the change point, (ϕ). The final term in $(x_i - \phi)_+$ is equal to $(x_i - \phi)$ if $x_i > \phi$, and 0 otherwise.

The models were estimated using Bayesian estimation and the program JAGS was used for all analyses (Plummer 2013), ran within R (Core Team 2013). After discarding the first 15,000 samples, we retained every 3rd sample for a total of 22,500 samples. We examined the scale reduction factor, a convergence statistic, for each parameter, trace plots, and plots of posterior distributions to assess convergence.

Genetic analysis

Fin tissue samples were obtained from wild brook trout from five of the study streams: Hunts Run (n = 36), McKinnon Branch (n = 48), McNuff Branch (n = 50), Rock Run (n = 50) and Whitehead Run (n = 50). We limited sampling to individuals greater than 100 mm to avoid sampling bias due to sampling related individuals from a limited number of families (Allendorf and Phelps 1981; Hudy et al. 2010). A total of 234 caudal fin clips (~1 cm²) were collected and stored individually in 95 % non-denatured ethanol until processing.

DNA extraction and genotyping

Genomic DNA from caudal fin clip tissue was extracted based on Kingfisher® Flex (Thermo Fisher Scientific, Inc., Vantaa, Finland) and PureGene® (Gentra Systems, Inc., Minneapolis, MN) extraction methods following the manufacturers guidelines. Following the PureGene protocols, the isolated DNA was resuspended in 100µl of 10 mM Tris-HCl, pH 8.0, 1 mM EDTA. Twelve microsatellite loci were selected for analysis: *SfoB52*, *SfoC24*, *SfoC28*, *SfoC38*, *SfoC79*, *SfoC86*, *SfoC88*, *SfoC113*, *SfoC115*, *SfoC129*, *SfoD75*, *SfoD91* and *SfoD100* (King et al. 2012). All loci were combined into three multiplexes for PCR amplification and electrophoresis depending on fragment size and fluorescent label. Each 15µl PCR consisted of 1.5µl of genomic DNA extract, 2.0–4.0 X PCR buffer (10 mM Tris-HCl, pH 8.3; 50 mM KCl), 1.5–3.0 mM MgCl₂, 1.3–2.5 mM each dNTP, 0.1µl to 0.8µl of each primer (forward primer fluorescently labeled with FAM, NED or HEX; Applied Biosystems, Foster City, CA), 0.1 units/µl 0.27 units/µl of Taq polymerase (Promega Corporation, Madison, WI), and deionized water added to achieve the final volume. The amplification cycle for all loci consisted of an initial denaturing at 94° C for 2 min; 35

cycles of 94° C denaturing for 45 s, 56° C annealing for 45 sec, 72° C extension for 2 min; and a 10 min extension at 72° C. An ABI Prism 3100® Genetic Analyzer (Applied Biosystems, Foster City, CA) was used for capillary electrophoresis. Alleles were individually-scored using GeneMapper® version 4.1 software (Applied Biosystems Inc.) using internal lane size standards.

Genetic statistical analysis

Conformance to Hardy-Weinberg equilibrium and measures of genetic diversity (allele frequencies, average number of alleles, and heterozygosities) were estimated for each population using the program GDA version 1.1 (Lewis and Zaykin 2002) and GenAIEx version 6.3 (Peakall and Smouse 2006). In addition, estimates of allelic richness and allelic variance were calculated through the program FSTAT (Goudet 2000).

The number of genetically homogeneous groups of individuals, or clusters (K) was determined using the program STRUCTURE (Pritchard et al. 2010). As described in Evanno et al. (2005), twenty runs were performed for each value of K with a length of burn-in and MCMC (Markov chain Monte Carlo) of 10,000 each. Multiple runs for each K were performed in order to quantify the amount of variation of the likelihood of each K. The range of possible K values tested was from 1 to 8. An ad hoc statistic (ΔK) based on log probability of the data was then calculated following (Evanno et al. 2005), and plotted.

Estimates of the effective population size (N_e) and 95 % jackknife confidence intervals were derived through the program LDNe version 1.31 (Waples and Do 2008) for each population based on all sampled individuals. Further, analyses of fish length frequency histograms (results not explicitly shown) indicated the possible presence of two year classes (e.g., <100 mm and >100mm) for individuals sampled in Hunts Run, McKinnon Branch and McNuff Branch. For brook trout populations, the presence of multiple year classes or cohorts can commonly occur as populations almost always have overlapping generations (Curry et al. 2010). N_e estimates obtained from mixed-cohorts samples might be biased low (Waples 2010). Therefore, to limit N_e estimates to single cohorts or age-classes possibly present, separate N_e estimates were derived for Hunts Run, McKinnon

Branch and McNuff Branch using sampled individuals > 100 mm within these populations. All N_e estimates were derived using a minimum allele frequency cut-off (P_{crit}) of 0.02, which has been shown to provide an adequate balance between precision and bias across different sample sizes (Waples and Do 2008). N_e estimates represent the size of an ideal population experiencing the same rate of change of allele frequencies or heterozygosity as the observed population of interest.

Pairwise F_{st} and associated p-values were derived based on allelic variance to estimate differences in allele frequencies between populations. Sequential Bonferroni adjustments (Rice 1989) were used to determine statistical significance ($P < 0.05$) due to multiple comparisons. Individual maximum-likelihood assignment probabilities to population of origin were calculated using GeneClass version 2.0 (Piry et al. 2004) to determine which population an individual's genotype was most likely to occur. The genetic relationship among the five populations analyzed were visualized through the program TreeView version 1.6.6 (Page 2001) as a consensus tree based on Cavalli-Sforza and Edwards (1967) produced in the program PHYLIP (Felsenstein 2002). The consensus tree was generated through performing 1,000 bootstrap resamplings over loci using Seqboot, Neighbor, and Consense software in the program PHYLIP.

Results

Stream summary statistics

Study streams ranged from 1st (Whitehead Run and Rock Run) to 5th (Driftwood Branch) order and

contained both sympatric brook trout and brown trout and allopatric brook trout populations (Table 1). Density of brown trout ranged from 129.8 kg/ha in Hunts Run to 0 kg/ha in Rock Run; whereas, density of brook trout ranged from 25.5 kg/ha in Whitehead Run to 5.2 kg/ha in McNuff Branch. Despite streams varying in size, all streams had a relatively similar proportion of pool habitat (Table 1).

Movement summary statistics

Fish were located two to three times per week between 16 September 2012 and 4 January 2013. From 5 January to 25 February 2013, fish were located approximately 1 to 2 times per week because the number of active transmitters and fish movement were greatly reduced. All radio-tracking concluded on 25 February 2013. A total of 2,045 fish locations were collected during the 163 day study period. The number of days a fish was tracked ranged from 13 – 163 d and the number of relocations collected on a fish ranged from 1 – 35. Brook trout movement between locations ranged from 0 – 4,533 m with a median of 5.3 m. Brown trout movement between locations ranged from 0 – 11,665 m with a median of 4 m. Maximum upstream movement was 1,112 m for brook trout and 3,462 m for brown trout. Maximum downstream movement was 10,145 m and 11,449 m for brook and brown trout, respectively. Mean total movement was higher for brown trout than for brook trout (mean ± SD total movement: brown trout = 2,924 ± 4,187 m; brook trout = 1,769 ± 2,194 m). Median total movement was similar among species: median total movement was 1,029 m for brown trout and 1,047 m for brook trout.

Table 1 Stream characteristics including stream order, distance from Driftwood Branch (Distance), average flow (collected between September 2012 – January 2013), trout density, and the proportion of pool and non-pool habitat (Habitat heterogeneity)

Stream	Stream order	Distance (km)	Average flow (m^3/s)	Trout density (kg/ha)	Habitat heterogeneity
Driftwood Branch	5	NA	3.93	ND	ND
Hunts Run	4	0.0	1.42	Brook (5.9); Brown (129.8)	Pool (47 %); Non-pool (53 %)
McKinnon Branch	2	0.2	0.27	Brook (8.2); Brown (16.7)	Pool (42 %); Non-pool (58 %)
McNuff Branch	2	8.4	0.22	Brook (5.2); Brown (14.6)	Pool (32 %); Non-pool (68 %)
Rock Run	1	4.8	ND	Brook (8.8)	Pool (29 %); Non-pool (71 %)
Whitehead Run	1	3.7	0.08	Brook (25.5); Brown (23.7)	Pool (33 %); Non-pool (67 %)

NA = not applicable; ND = data not available

Temporal dynamics

Temporal movement dynamics for both species was similar (Fig. 2). There were two noticeable peaks in movement that corresponded to the spawning season and increases in stream flow (see Effects of covariates on movement). There was also an overall trend of upstream movement during the fall (e.g., September – November) followed by a general downstream movement through early winter (e.g., December and January). Specifically, brook trout tended to move upstream between September and October and downstream between November and December; whereas, brown trout tended to move upstream through November and downstream between December and January.

Effects of covariates on movement

There was substantial variability among fish in average \log_e movement, residual SD and average \log_e movement among streams (Fig. 3). Partitioning the total variance in \log_e movement among fish, streams, and residual standard error showed that a majority of the variability was contained in the residual error

term: 83.8 % (95 % credible interval [CRI] = 60.0 %, 91.9 %) was residual error, 7.4 % (95 % CRI = 4.1 %, 11.6 %) was among fish, and 8.8 % (95 % CRI = 1.4 %, 34.4 %) was among streams. There was, on average, a trend towards more movement in the larger streams (e.g., Hunts Run and McKinnon Branch compared to smaller streams such as Rock Run; Fig. 3c). Brook trout \log_e movement between locations was, on average, larger when compared to brown trout (95 % CRI of difference in \log_e movement between species did not overlap zero; 95 % CRI = 0.030, 0.66). There was, however, no difference in average residual standard deviation between brook and brown trout (95 % CRI of difference in σ = -0.122, 0.355). There was a threshold effect of flow on movement, but not temperature, with movement increasing after a positive increase in flow occurred ($\hat{\phi}$ = 0.00, 95 % CRI = [-0.17, 0.19]; Fig. 4). There was no difference in the threshold response between brook and brown trout (all 95 % CRIs for the differences between species in β_0 , β_1 , δ , and ϕ overlapped zero). There was also a positive effect of \log_e fish weight on fish-specific standard deviations (Fig. 5) and this relationship was consistent for brook and brown trout (95 % CRI for the difference

Fig. 2 Movement (\log_e -transformed) of brook and brown trout **a**, brook trout only **b** and brown trout only **c**. Points are observations of movement, solid line is posterior mean fitted line from a dynamic linear model (see Methods). Arrows indicate high-flow events and correspond to spawning season (October – December)

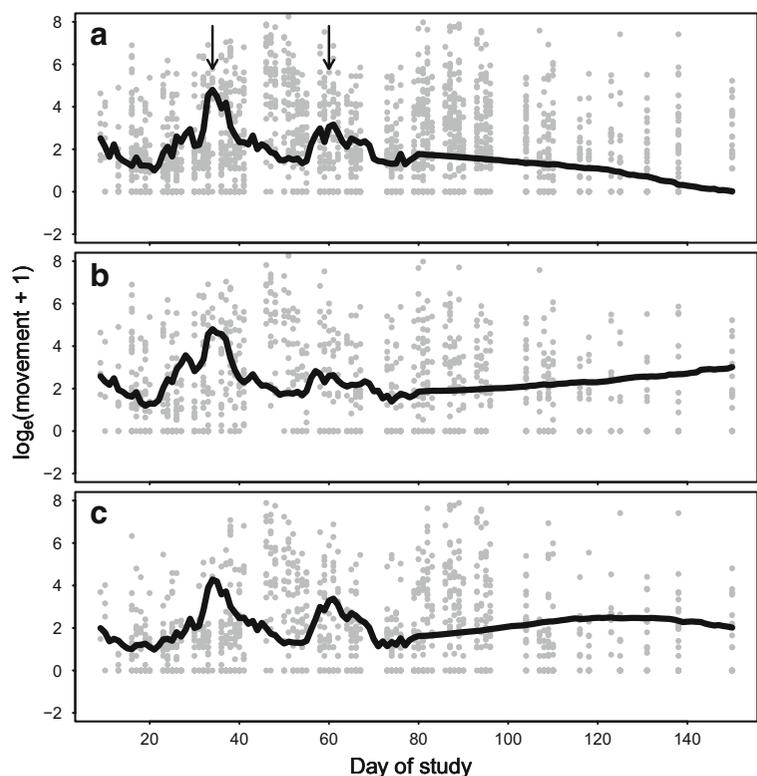
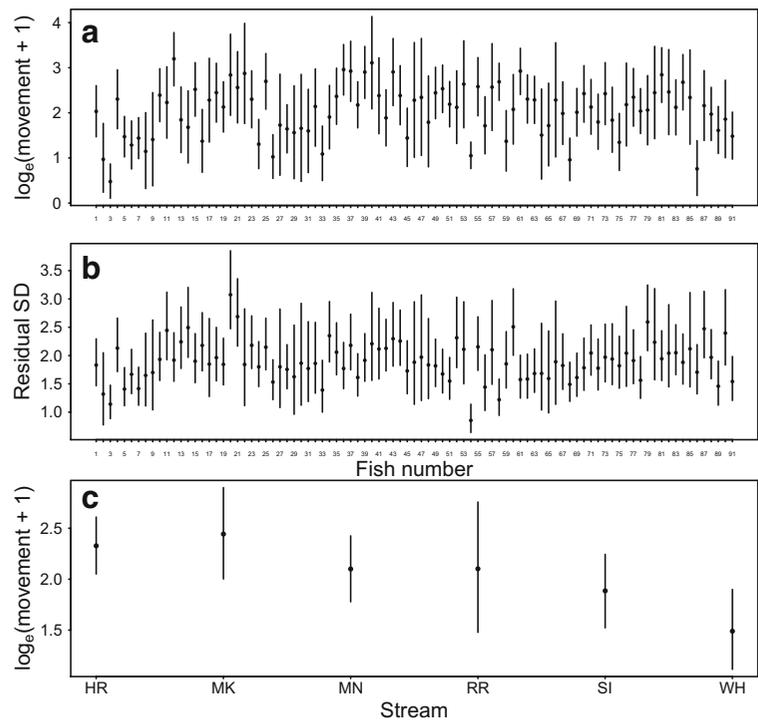


Fig. 3 Fish-specific (brook and brown trout) movement (\log_e -transformed; **a**) and residual standard deviations **b** and stream specific movement estimates **c**. Points are posterior means and vertical bars are 95 % credible intervals



between species-specific slopes of the relationship between \log_e weight and fish-specific standard deviations = -0.16, 0.26). There was no effect, however, of fish size on fish-specific average movements.

Genetic analysis – within population genetic diversity

All twelve microsatellites were polymorphic, with the number of alleles ranging from 4 (*SfoC38*) to 18 (*SfoC115*, *SfoD91*; Online Resource 1). The overall mean allelic richness was 8.193, and varied from 7.813 in McNuff Branch to 8.500 in Hunts Run (Table 2). Estimates of average observed heterozygosity differed minimally (< 0.041) than those expected under Hardy-Weinberg equilibrium (Table 2). A few deviations from Hardy-Weinberg equilibrium were present including six locus-pairs from McNuff Branch (*SfoB52/SfoC129*, *SfoB52/SfoD75*, *SfoC24/SfoD75*, *SfoC115/SfoD75* and *SfoC129/SfoD75*) and a single locus (*SfoC88*) and locus-pair (*SfoC88/SfoD91*) from Rock Run. However, deviations were not consistent across the populations indicating an absence of null alleles. Thirteen private alleles occurred including two from Hunts Run, six from McKinnon Branch, three from McNuff Branch and two

from Whitehead Run. However, overall frequencies of the private alleles were low, ranging from 1 % (*SfoC115* allele 235, 245 and *SfoD91* allele 288) to 3.1 % (*SfoD100* allele 242). The overall average observed heterozygosity was 0.734, and ranged from 0.704 in Hunts Run to 0.758 in Whitehead Run (Table 2).

Effective population size estimates were highest for Hunts Run and McKinnon Branch populations indicating that the number of spawning adult Brook Trout would be highest for these two populations (Table 3). Effective population size estimates were small for McNuff Branch, Rock Run and Whitehead Run (Table 3). For the samples obtained from individuals > 100 mm in total length, analyses based on length-frequency revealed the possible presence of two year-classes within the sampled individuals from Hunts Run, McKinnon Branch, and McNuff Branch. For samples collected in Hunts Run, \widehat{N}_e were greater for individuals > 100 mm sampled ($\widehat{N}_e = 234.4$, Table 3) than estimates derived from all individuals sampled ($\widehat{N}_e = 99.4$; Table 3) indicating an effect of year class on \widehat{N}_e . However, for individuals sampled in McKinnon Branch and McNuff Branch, N_e were similar across the two year-classes analyzed indicating no

Fig. 4 Relationship between brook and brown trout movement and change in stream flow. Points are individual observations, solid line is posterior mean fitted line, shaded region is 95 % credible region, open red point and horizontal line are estimated change point and associated 95 % credible interval, respectively

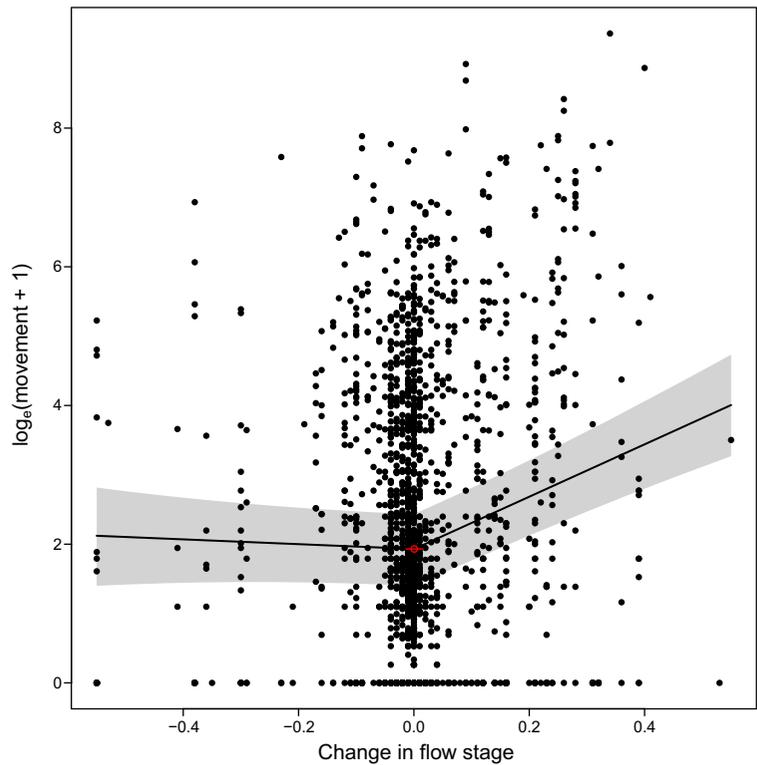


Fig. 5 Relationship between variability in fish-specific movement (fish-specific residual standard deviation [SD]) and fish weight (\log_e -transformed; g). Points are posterior means, vertical lines are 95 % credible intervals, solid line is hierarchical fitted line and shaded region is 95 % credible region

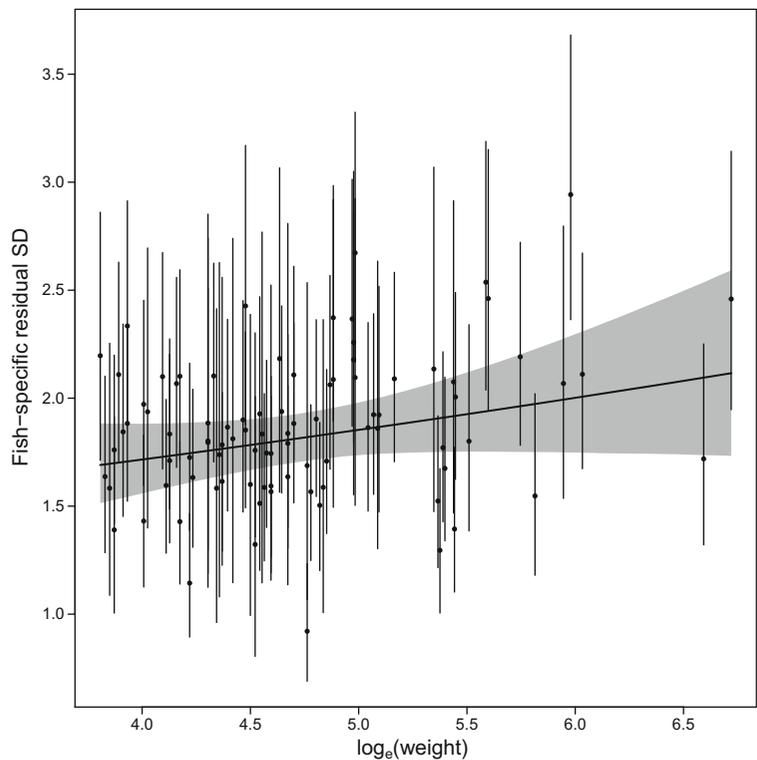


Table 2 Site abbreviations, sample size (N), observed heterozygosity (H_o), expected heterozygosity (H_e), mean number of alleles per locus (A), mean allelic richness (A_r), and mean inbreeding coefficient (F_{is})

Site	Abbreviation	N	H_o	H_e	A	A_r	F_{is}
Hunts Run	HR	36	0.704	0.743	8.5	8.5	0.054
McKinnon Branch	MK	48	0.717	0.736	8.75	8.315	0.026
McNuff Branch	MN	50	0.743	0.758	8.167	7.813	0.02
Rock Run	RR	50	0.747	0.752	8.333	8.092	0.007
Whitehead Run	WH	50	0.758	0.757	8.583	8.247	-0.001

effect of separate cohort analyses on N_e and therefore estimates represent the entire sample for the study populations of McKinnon Branch, McNuff Branch, Rock Run, and Whitehead Run.

Genetic analysis – among population genetic diversity

Result from STRUCTURE analyses indicated the number of distinct genetic clusters (K) to be 2 (ΔK). Analyses of genetic difference in allele frequencies among populations revealed significant ($P < 0.05$) genetic differentiation between all five study populations (Table 4), following Bonferroni corrections for multiple comparisons. The overall mean genetic differentiation was $F_{st} = 0.020$. The allelic frequency differentiation was greatest between Rock Run and McNuff Branch populations ($F_{st} = 0.040$; Table 4), and lowest between Rock Run and Whitehead Run populations ($F_{st} = 0.002$; Table 4). Results from GeneClass assignment test was consistent with the observed differences in allelic frequency differences (or lack thereof), and revealed the frequency of self-assignment ranging from 50 % in Rock Run to 78 %

in McNuff Branch (Table 4). A large proportion (44 %) of individuals in Rock Run assigned to Whitehead Run. Furthermore, 28 % of individuals sampled in Whitehead Run assigned to Rock Run (Table 5). McNuff Branch had the highest self-assignment value (78 %), consistent with the greatest pairwise F_{st} values observed between McNuff Branch and each of the other populations (Table 4). Hunts Run had the lowest self-assignment value (41 %, Table 5) and lowest F_{st} values for Hunts Run were observed with McKinnon Branch (Table 4).

Results from the neighboring-joining tree (Fig. 6) indicated that Rock Run and Whitehead Run were genetically similar to each other, being grouped as nearest neighbors in 100 % of replicates (i.e., 1000/1000 replicates). Hunts Run was found to be genetically similar to McKinnon Branch and McNuff Branch. However, the relatedness between Hunts Run and McKinnon Branch was weakly supported, with grouping occurring in only slightly more than half the replicates (e.g., 578/1000). McNuff Branch was found to be least similar to Rock Run and Whitehead Run (Fig. 6).

Table 3 Estimates ($\widehat{N_e}$) and 95 % jackknife confidence intervals for the effective population size for all brook trout and brook trout > 100 mm sampled from Hunts Run, McKinnon Branch and McNuff Branch in the Hunts Run Watershed, PA

	Hunts Run	McKinnon Branch	McNuff Branch	Rock Run	Whitehead Run
<u>All fish</u>					
$\widehat{N_e}$	99.4	73.5	32.2	27.4	36.9
95 % CI	60.4 - 234.4	51.7 - 117.6	26.7 - 39.4	23.7 - 32.5	31.3 - 44.2
<u>≥100 mm fish</u>					
$\widehat{N_e}$	234.4	72.5	27.7	NA	NA
95 % CI	78.8 - Inf.	43.6 - 175	22.9 - 34.1		

Estimates are based minimum allele frequency cutoff of 0.02

Table 4 Matrix displaying pairwise F_{st} values. All pairwise F_{st} values were significant ($\alpha < 0.05$) after sequential Bonferroni corrections

Site	HR	MK	MN	RR	WH
Hunts Run (HR)	0	-	-	-	-
McKinnon Branch (MK)	0.007	0	-	-	-
McNuff Branch (MN)	0.015	0.016	0		-
Rock Run (RR)	0.02	0.031	0.04	0	
Whitehead Run (WH)	0.017	0.022	0.031	0.002	0

Discussion

Fish movement

Stream fishes, and stream-dwelling salmonids in particular, are often characterized by a large amount of variability in movement dynamics (Mollenhauer et al. 2013). Temporally, we found that movements corresponded to the spawning season for both brook and brown trout and occurred during positive flow events. These findings are similar to those presented in other radio telemetry studies evaluating the seasonal movements of salmonids. For example, (Curry et al. 2002) reported increased activities and movements by brook trout in the fall. In addition, long-range movements (up to tens of km) by brown trout during the fall spawning season have been reported (Clapp et al. 1990; Young 1994). Moreover, increased seasonal activities by both species have also been shown during the use of mark-recapture and weir sampling (Petty et al. 2005; Gowan and Fausch 1996). The majority of movement by both species occurred during two high flow events. The influence of flow on movement has

been reported in several studies (Clapp et al. 1990; Young 1994; Dare et al. 2002; Mollenhauer et al. 2013). For instances, (Mollenhauer et al. 2013) found a positive correlation between fall/early winter brook trout movement and stream flow. In addition, long-range movements by brown trout were found to occur during high water events (Clapp et al. 1990).

While there was temporal dynamics in movement and effects of flow on the movements of both species, there was also notable variability among individuals in their movement patterns. For example, some individuals were regularly more active throughout the study period whereas others moved minimally; although larger fish showed higher amounts of variability in movement. This variability in movement among fish has been documented in both brook trout and brown trout. In a radio telemetry study completed by Roghair and Dolloff (2005) seasonal movement of brook trout varied among individuals, with the majority of brook trout moving less than 100 m and a few individuals moving greater than 800 m. Similar results in movement heterogeneity among individual brook trout was also observed in radio

Table 5 The proportional assignment for 234 brook trout and 5 site locations represented in the Hunts Run Watershed, PA, and the sum of individuals sampled for each site

Site	HR	MK	MN	RR	WH	Sum
Hunts Run (HR)	0.417	0.167	0.194	0.111	0.111	36
McKinnon Branch (MK)	0.083	0.646	0.146	0.042	0.083	48
McNuff Branch (MN)	0.12	0.1	0.78	0	0	50
Rock Run (RR)	0.04	0.02	0	0.5	0.44	50
Whitehead Run (WH)	0.1	0.02	0.04	0.28	0.56	50

Assignments were based on genotypic frequencies at 12 microsatellite loci. The diagonal represents the proportion of individuals that were assigned back to their sample site-of-origin. Column headings represent population assigned from, and row labels represents stream classified to

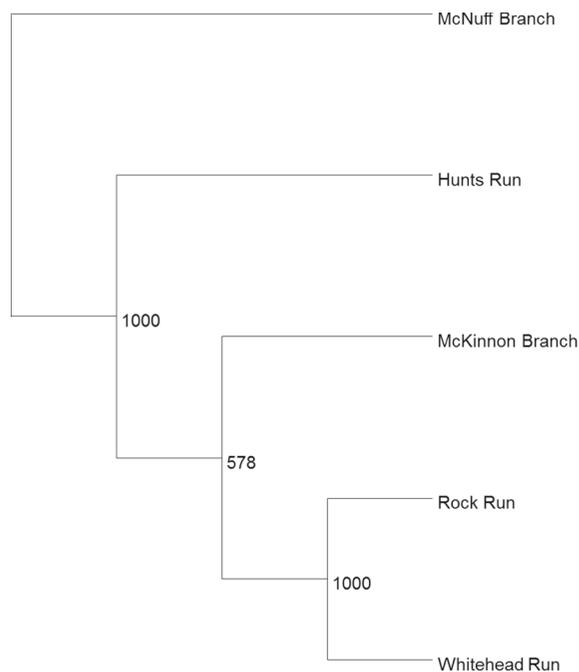


Fig. 6 Neighboring-joining tree representing the genetic divergence among five brook trout populations located in the Hunts Run Watershed, PA. Tree is based on Cavalli-Sforza and Edwards (1967) chord distances, and numbers represent bootstrap values over 1,000 replicates

telemetry study conducted by Mollenhauer et al. (2013). In addition, (Burrell et al. 2000) observed variation among individuals in seasonal brown trout movement, with movement between individuals ranging from 206 m to 7.6 km during the spawning season. Some studies have attributed this among-individual variation in movement to difference in life history strategies between large and small fish or river and stream migrants, respectively (Garrett and Bennett 1995; Young 1994). However, unlike these studies we observed long-range (> 2.5 km) movements across a range of size classes (e.g., 175 to 430 mm and 49 to 829 g). In addition, similar to findings by Petty et al. (2012), we observed a general trend of increased mobility among mainstream (e.g., Hunts Run and McKinnon Branch) fish compared to fish in smaller tributaries (e.g., Whitehead Run).

Genetic analysis

Results from the brook trout genetics analysis were congruent with movement data obtained using radio

telemetry. Analyses for genetic differentiation (e.g., F_{st} values) revealed significant but generally low differences between all five study streams (populations), indicating that there may be up to five spawning populations with varying levels of gene flow between streams. For example, the similarities between Whitehead Run and Rock Run, and McKinnon Branch and Hunts Run indicate that there is likely some greater degree of gene flow between those spawning areas than between the other streams. While these measures of genetic differentiation are statistically significant, they may have biological significance resulting from low levels of migration within the Hunts Run Watershed. Population genetic theory suggests that one migrant per generation can reduce population differentiation, and depending on the reproductive success of that migrant and the population size can in some cases result in a failure to detect genetic differentiation among populations (Allendorf and Phelps 1981; Mills and Allendorf 1996; Wang 2004).

In addition, poor individual maximum-likelihood assignment probabilities to population of origin were observed overall. The deficiency of individuals assigned correctly to their population of origin reflects the observed low level of population differentiation (pairwise F_{st}). A high frequency of self-assignment usually occurs for populations that are more genetically divergent (Sønstebo et al. 2007). The mis-assignment of individuals sampled in Rock Run that assigned to Whitehead Run occurred at a frequency of approximately 44 %, consistent with results from the neighboring joining tree: where 100 % of replications grouped Rock Run and Whitehead Run as nearest neighbors. These two populations were also the least divergent (e.g., $F_{st} = 0.002$) in comparison to all other populations, revealing some level of gene exchange that is likely the result of movement of individuals between these two streams. Tagging observations identified one brook trout from Rock Run moving downstream into Whitehead Run in mid-November, suggesting that movement and gene flow between these two populations may occur. In addition, results from neighboring joining tree and the individual assignment test examining the relatedness of McKinnon Branch and Hunts Run were consistent and agreed with telemetry-based movement findings. For example, McKinnon Branch and Hunts Run were found to be nearest neighbors, with more than 16 % of individuals sampled in

Hunts Run mis-assigned to McKinnon Branch. Three radio-tagged brook trout in McKinnon Branch were documented to move downstream into Hunts Run between October 2012 and December 2012. These types of among-stream movements may explain the mis-assignments and grouping of these two as their nearest genetic neighbor in the neighbor joining tree.

The observed levels of within population genetic variability further supports the gene flow observed within the Hunts Run Watershed. Small, isolated populations typically have reduced genetic variability as a result of genetic drift and inbreeding effects (Consuegra et al. 2005; Kanno et al. 2011). Because effective population size allows for the determination of the degree of genetic drift and effectiveness of natural selection it is important to evaluate. Also, observed levels of within population genetic variability may also indicate self-sustaining population sizes potentially due to an absence of population bottlenecks for study populations (Jones et al. 1997). Although populations demonstrate a moderate amount of genetic variation, estimates of effective population size were low for McNuff Branch, Rock Run and Whitehead Run ($\widehat{N}_e < 37$). A commonly referenced rule of thumb for minimum effective population size required to maintain genetic diversity is an $N_e \geq 50$ individuals for short-term conservation and heterogeneity and an $N_e \geq 500$ individuals for more long-term considerations (Franklin 1980). Similar findings of reduced genetic differentiation among tributary populations related to effective migration has been found (Aunins et al. 2015; Kelson et al. 2015). While evidence for the effect of multiple year classes on \widehat{N}_e was insufficient for most locations, the bias observed between size based cohorts in Hunts Run indicated that N_e estimates may be biased low, consistent with other findings (Whiteley et al. 2010). In consideration with other results including population classification, likely Hunts Run represents an admixed population with individuals either directly from other populations or offspring resulting from reproduction in Hunts Run by individuals originating from other locations. Operating then as an open population, the N_e estimates for Hunts Run would be inflated. Given the increased populations, and the gene flow and migration into Hunts Run, the population is more likely to maintain genetic diversity for a longer period of time in comparison to the other, smaller populations, or

at minimum serve as a source for genetic diversity for the other populations sampled. Additionally, the same closed population assumption is necessary under Hardy-Weinberg equilibrium. However, few deviations from Hardy-Weinberg equilibrium were actually observed.

Overall, the true number of genetically homogeneous groups of individuals or clusters present was determined to be two. However, when calculating ΔK , two is the lowest possible value that can be given for the estimate of the true number of groups (Evanno et al. 2005). Therefore, it is possible that the true number of groups may be one within the Hunts Run Watershed. This is a reasonable assumption given the low genetic variances between populations as well as observations in brook trout movement. As no obvious potential barriers to movement exist within the Hunts Run Watershed, brook trout possess the ability to move freely between streams. It is also apparent given the genetic data and observations in movement that some individual brook trout do move between streams in the Hunts Run Watershed. Given the small effective population sizes for some of the populations sampled, these brook trout populations are considered small. The fecundity, juvenile survival and life span of individuals within these populations may be negatively affected as a result of losses in genetic diversity that can possibly lead to complete extirpation (Frankham and Ralls 1998). However, the ability of brook trout to move among streams can play a large role in the persistence of existing brook trout populations to offset threats to brook trout that may continue to isolate and reduce populations to headwater reaches. Likely, these populations interact with some low level of gene flow which helps to maintain populations within each tributary, maintain genetic diversity to offset decreases due to inbreeding and small population sizes, and therefore they operate to some degree as a metapopulation within the watershed.

Conclusions

Temporal variations in movement observed by both brook and brown trout highlight the importance of maintaining (or restoring) stream connectivity. The ability of fish to maximize individual fitness (i.e., survival, reproductive success and growth) has been found to be dependent on the ability of fish to respond

through movement to temporal variations in habitat requirements (Chisholm et al. 1987; Fausch et al. 2002; Young et al. 2010). In addition, a large-scale perspective including multiple streams may also be important for managing existing populations as long range movements within and among study streams have been observed. This large-scale perspective may aid in the management of populations within special regulation streams and reaches. For instance, as observed in this study, trout may move out of reaches that are managed under a catch-and-release regulation and into reaches or streams open to harvest. This could potentially have an influence on successful management of these populations, depending on the fishing pressure, harvest rate, and the number of individuals that complete these movements out of special regulation areas.

The maintenance of stream connectivity is also important as it may allow for recolonization following extirpation (Roghair and Dolloff 2005) as well as improve genetic diversity by preventing populations from becoming isolated (D'Amelio et al. 2008), which can aid management agencies in maintaining viable populations into the future. However, it is important recognize that some streams or stream reaches may recolonize at different rates, given the observed heterogeneity in fish movement observed among our study streams. A watershed approach, opposed to managing streams as discrete reaches, may help managers in addressing and maintaining stream connectivity while helping to improve understanding on the recolonization potential within an entire system of interconnected streams (Roghair and Dolloff 2005; Letcher et al. 2007). As trout populations continue to be threatened by a myriad of anthropogenic activities that may result in increased habitat degradation, a watershed approach to managing existing populations may be vital as populations are becoming increasingly isolated or restricted especially in headwater stream reaches.

Acknowledgments We thank Jason Detar, Dave Kristine, and John Sweka for assisting with field sampling, and Josh Hickey, Evan Faulk, and Zeb Buck for assisting with radio tracking. We also thank Shannon Julian for assistance with genetic analyses and Todd Petty for helpful comments on an earlier draft of this manuscript. Finally, we thank the Pennsylvania District of Conservation and Natural Resources (Steve VanEerden) for allowing access to their property to conduct this research.

Funding was provided by the U.S. Geological Survey and the Pennsylvania Fish and Boat Commission. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The handling of fish followed protocols approved by The Pennsylvania State University Institutional Animal Care and Use Committee (IACUC # 35254). The findings and conclusions in this article are those of the author(s) and not necessary represent the views of the U.S. Fish and Wildlife Service.

References

- Adams SB, Frissell CA, Rieman BE (2000) Movements of nonnative brook trout in relation to stream channel slope. *Trans Am Fish Soc* 129(3):623–638. doi:[10.1577/1548-8659\(2000\)129%3C0623:monbti%3E2.3.co;2](https://doi.org/10.1577/1548-8659(2000)129%3C0623:monbti%3E2.3.co;2)
- Allendorf FW, Phelps SR (1981) Use of allelic frequencies to describe population structure. *Can J Fish Aquat Sci* 38(12):1507–1514. doi:[10.1139/f81-203](https://doi.org/10.1139/f81-203)
- Angers B, Bernatchez L, Angers A, Desgroseillers L (1995) Specific microsatellite loci for brook charr reveal strong population subdivision on a microgeographic scale. *J Fish Biol* 47:177–185. doi:[10.1111/j.1095-8649.1995.tb06054.x](https://doi.org/10.1111/j.1095-8649.1995.tb06054.x)
- Aunins A, Petty KT, Schilz M, Mazik P (2015) River mainstem thermal regimes influence population structuring within an appalachian brook trout population 16(1):15–29. doi:[10.1007/s10592-014-0636-6](https://doi.org/10.1007/s10592-014-0636-6)
- Ayllón D, Nicola GG, Elvira B, Parra I, Almodóvar A (2013) Thermal carrying capacity for a thermally-sensitive species at the warmest edge of its range. *PLoS ONE* 8(11):e81,354+. doi:[10.1371/journal.pone.0081354](https://doi.org/10.1371/journal.pone.0081354)
- Burrell KH, Isely JJ, Bunnell DB, Van Lear DH, Dolloff CA (2000) Seasonal movement of brown trout in a southern Appalachian river. *Trans Am Fish Soc* 129(6):1373–1379. doi:[10.1577/1548-8659\(2000\)129%3C1373:smobti.%3E2.0.co;2](https://doi.org/10.1577/1548-8659(2000)129%3C1373:smobti.%3E2.0.co;2)
- Cavalli-Sforza LL, Edwards AW (1967) Phylogenetic analysis. models and estimation procedures. *Am J Hum Genet* 19(3 Pt 1):233–257. <http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1706274/>
- Chisholm IM, Hubert WA, Wesche TA (1987) Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. *Trans Am Fish Soc* 116(2):176–184. doi:[10.1577/1548-8659\(1987\)116%3C176:wscאו%3E2.0.co;2](https://doi.org/10.1577/1548-8659(1987)116%3C176:wscאו%3E2.0.co;2)
- Clapp DF, Clark RD, Diana JS (1990) Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. *Trans Am Fish Soc* 119(6):1022–1034. doi:[10.1577/1548-8659\(1990\)119%3C1022:rahol%3E2.3.co;2](https://doi.org/10.1577/1548-8659(1990)119%3C1022:rahol%3E2.3.co;2)
- Consuegra S, Verspoor E, Knox D, García de Leániz C (2005) Asymmetric gene flow and the evolutionary maintenance of genetic diversity in small, peripheral Atlantic salmon populations. *Conserv Genet* 6(5):823–842. doi:[10.1007/s10592-005-9042-4](https://doi.org/10.1007/s10592-005-9042-4)

- Curry Bernatchez L, Whoriskey F, Audet C (2010) The origins and persistence of anadromy in brook charr. *Rev Fish Biol Fish* 20(4):557–570. doi:10.1007/s11160-010-9160-z
- Curry RA, Sparks D, van de Sande J (2002) Spatial and temporal movements of a riverine brook trout population. *Trans. Am. Fish. Soc.* 131(3):551–560. doi:10.1577/1548-8659(2002)131%3C0551:satmoa%3E2.0.co;2
- D'Amelio S, Mucha J, Mackereth R, Wilson CC (2008) Tracking coaster brook trout to their sources: combining telemetry and genetic profiles to determine source populations. *N Am J Fish Manag* 28(4):1343–1349. doi:10.1577/m05-193.1
- Dare MR, Hubert WA, Gerow KG (2002) Changes in habitat availability and habitat use and movements by two trout species in response to declining discharge in a regulated river during winter. *N Am J Fish Manag* 22(3):917–928. doi:10.1577/1548-8675(2002)022%3C0917:cihaah%3E2.0.co;2
- DeGrandchamp KL, Garvey JE, Colombo RE (2008) Movement and habitat selection by invasive Asian carps in a large river. *Trans Am Fish Soc* 137(1):45–56. doi:10.1577/t06-116.1
- EBTJV (2011) Conserving the Eastern Brook Trout: Action Strategies. Tech. rep., Eastern Brook Trout Joint Venture, 350 Hunkins Pond Road, Sanbornton, NH
- Eby LA, Helmy O, Holsinger LM, Young MK (2014) Evidence of climate-induced range contractions in bull trout *Salvelinus confluentus* in a Rocky Mountain Watershed, U.S.A. *PLoS ONE* 9(6):e98,812+. doi:10.1371/journal.pone.0098812
- Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Mol Ecol* 14(8):2611–2620. doi:10.1111/j.1365-294x.2005.02553.x
- Fausch KD, White RJ (1981) Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Can J Fish Aquat Sci* 38(10):1220–1227. doi:10.1139/f81-164
- Fausch KD, Torgersen CE, Baxter CV, Li HW (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52(6):483–498. doi:10.1641/0006-3568(2002)052%5B0483:lrbtbg%5D2.0.co;2
- Felsenstein J (2002) PHYLIP (Phylogeny Inference Package) version 3.6a3. Distributed by the author. Department of Genome Sciences, University of, Washington, Seattle
- Frankham R, Ralls K (1998) Conservation biology: Inbreeding leads to extinction. *Nature* 392(6675):441–442. doi:10.1038/33022
- Franklin IR (1980) Evolutionary change in small populations. Sinauer Associates, Inc., 23 Plumtree Road, 135–150 http://books.google.com/books/about/Conservation_biology.html?id=YPgTAQAIAAJ
- Garrett JW, Bennett DH (1995) Seasonal movements of adult brown trout relative to temperature in a cool-water reservoir. *N Am J Fish Manag* 15(2):480–487. doi:10.1577/1548-8675(1995)015%3C0480:smoabt%3E2.3.co;2
- Goudet J (2000) FSTAT: A program to estimate and test gene diversities and fixation indices, version 2.9.1
- Gowan C, Fausch KD (1996) Mobile brook trout in two high-elevation Colorado streams: reevaluating the concept of restricted movement. *Can J Fish Aquat Sci* 53(6):1370–1381. doi:10.1139/f96-058
- Grant GC, Vondracek B, Sorensen PW (2002) Spawning interactions between sympatric brown and brook trout may contribute to species replacement. *Trans Am Fish Soc* 131(3):569–576. doi:10.1577/1548-8659(2002)131%3C0569:sibsba%3E2.0.co;2
- Hudy M, Coombs JA, Nislow KH, Letcher BH (2010) Dispersal and within-stream spatial population structure of brook trout revealed by pedigree reconstruction analysis. *Trans Am Fish Soc* 139:1276–1287. <http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.176.2901>
- Jones MW, Danzmann RG, Clay D (1997) Genetic relationships among populations of wild resident, and wild and hatchery anadromous brook charr. *J Fish Biol* 51(1):29–40. <http://view.ncbi.nlm.nih.gov/pubmed/9236086>
- Kanno Y, Vokoun JC, Letcher BH (2011) Fine-scale population structure and riverscape genetics of brook trout (*Salvelinus fontinalis*) distributed continuously along headwater channel networks. *Mol Ecol* 20(18):3711–3729. doi:10.1111/j.1365-294x.2011.05210.x
- Kanno Y, Letcher BH, Coombs JA, Nislow KH, Whiteley AR (2014) Linking movement and reproductive history of brook trout to assess habitat connectivity in a heterogeneous stream network. *Freshw Biol* 59(1):142–154. doi:10.1111/fwb.12254
- Kelson S, Kapuscinski A, Timmins D, Ardren W (2015) Fine-scale genetic structure of brook trout in a dendritic stream network 16(1):31–42. doi:10.1007/s10592-014-0637-5
- King TL, Lubinski BA, Burnham-Curtis MK, Stott W, Morgan RP (2012) Tools for the management and conservation of genetic diversity in brook trout (*Salvelinus fontinalis*): tri- and tetranucleotide microsatellite markers for the assessment of genetic diversity, phylogeography, and historical demographics 4(3):539–543. doi:10.1007/s12686-012-9603-z
- Letcher BH, Nislow KH, Coombs JA, O'Donnell MJ, Dubreuil TL (2007) Population response to habitat fragmentation in a stream-dwelling brook trout population. *PLoS ONE* 2(11):e1139+. doi:10.1371/journal.pone.0001139
- Lewis P, Zaykin D (2002) Genetic data analysis (GDA): computer program for the analysis of allelic data, version 1.1 <http://www.eeb.uconn.edu/people/plewis/software.php>
- Malmqvist B, Rundle S (2002) Threats to the running water ecosystems of the world. *Environmental Conservation* null:134–153. doi:10.1017/s0376892902000097
- Mills LS, Allendorf FW (1996) The one-migrant-per-generation rule in conservation and management. *Conserv Biol* 10(6):1509–1518. doi:10.1046/j.1523-1739.1996.10061509.x
- Mollenhauer R, Wagner T, Kepler MV, Sweka JA (2013) Fall and early winter movement and habitat use of wild brook trout. *Trans Am Fish Soc* 142(5):1167–1178. doi:10.1080/00028487.2013.793611

- Page RDM (2001) TreeView version 1.6.6. University of Glasgow Glasgow. Taxonomy.zoology.gla.ac.uk/rod/treeview.html
- Peakall R, Smouse PE (2006) Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. *Mol Ecol Notes* 6(1):288–295. doi:[10.1111/j.1471-8286.2005.01155.x](https://doi.org/10.1111/j.1471-8286.2005.01155.x)
- Petty JT, Lamothe PJ, Mazik PM (2005) Spatial and seasonal dynamics of brook trout populations inhabiting a Central Appalachian watershed. *Trans Am Fish Soc* 134(3):572–587. doi:[10.1577/t03-229.1](https://doi.org/10.1577/t03-229.1)
- Petty JT, Hansbarger JL, Huntsman BM, Mazik PM (2012) Brook trout movement in response to temperature, flow, and thermal refugia within a complex appalachian riverscape. *Trans Am Fish Soc* 141(4):1060–1073. doi:[10.1080/00028487.2012.681102](https://doi.org/10.1080/00028487.2012.681102)
- Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A (2004) A software for genetic assignment and first-generation migrant detection. *J Hered* 95:536–539
- Plummer M (2013) Rjags: Bayesian graphical models using MCMC
- Pritchard JK, Wen X, Falush D (2010) Documentation for structure software: Version 2.3
- Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43(1):223–225
- Roghair CN, Dolloff CA (2005) Brook trout movement during and after recolonization of a naturally defaunated stream reach. *N Am J Fish Manag* 25(3):777–784. doi:[10.1577/m04-034.1](https://doi.org/10.1577/m04-034.1)
- Ross MJ, Kleiner CF (1982) Shielded-needle technique for surgically implanting radio-frequency transmitters in fish. *The Progressive Fish-Culturist* 44(1):41–43. doi:[10.1577/1548-8659\(1982\)44%5B41:stfsir%5D2.0.co;2](https://doi.org/10.1577/1548-8659(1982)44%5B41:stfsir%5D2.0.co;2)
- Sgrò CM, Lowe AJ, Hoffmann AA (2011) Building evolutionary resilience for conserving biodiversity under climate change. *Evol Appl* 4(2):326–337. doi:[10.1111/j.1752-4571.2010.00157.x](https://doi.org/10.1111/j.1752-4571.2010.00157.x)
- Sønstebø JH, Borgstrøm R, Heun M (2007) Genetic structure of brown trout (*Salmo trutta* L.) from the Hardangervidda mountain plateau (Norway) analyzed by microsatellite DNA: a basis for conservation guidelines. *Conserv Genet* 8(1):33–44. doi:[10.1007/s10592-006-9145-6](https://doi.org/10.1007/s10592-006-9145-6)
- Spruell P, Rieman BE, Knudsen KL, Utter FM, Allendorf FW (1999) Genetic population structure within streams: microsatellite analysis of bull trout populations. *Ecol Freshw Fish* 8(3):114–121. doi:[10.1111/j.1600-0633.1999.tb00063.x](https://doi.org/10.1111/j.1600-0633.1999.tb00063.x)
- Steiner L (2000) Pennsylvania Fishes, Pennsylvania Fish and Boat Commission, P.O.Box 6700
- Stranko SA, Hilderbrand RH, Morgan RP, Staley MW, Becker AJ, Roseberry-Lincoln A, Perry ES, Jacobson PT (2008) Brook trout declines with land cover and temperature changes in Maryland. *N Am J Fish Manag* 28(4):1223–1232. doi:[10.1577/m07-032.1](https://doi.org/10.1577/m07-032.1)
- Wagner T, Deweber JT, Detar J, Sweka JA (2013a) Landscape-scale evaluation of asymmetric interactions between brown trout and brook trout using two-species occupancy models. *Trans Am Fish Soc* 142(2):353–361. doi:[10.1080/00028487.2012.734892](https://doi.org/10.1080/00028487.2012.734892)
- Wagner T, Irwin BJ, Bence JR, Hayes DB (2013b) Detecting temporal trends in freshwater fisheries surveys: statistical power and the important linkages between management questions and monitoring Objectives. *Fisheries* 38(7):309–319. doi:[10.1080/03632415.2013.799466](https://doi.org/10.1080/03632415.2013.799466)
- Wang J (2004) Application of the one-migrant-per-generation rule to conservation and management. *Conserv Biol* 18(2):332–343. doi:[10.1111/j.1523-1739.2004.00440.x](https://doi.org/10.1111/j.1523-1739.2004.00440.x)
- Waples RS (2010) Spatial-temporal stratifications in natural populations and how they affect understanding and estimation of effective population size. *Mol Ecol Resour* 10(5):785–796. <http://view.ncbi.nlm.nih.gov/pubmed/21565090>
- Waples RS, Do C (2008) Idne: a program for estimating effective population size from data on linkage disequilibrium. *Mol Ecol Resour* 8(4):753–756. doi:[10.1111/j.1755-0998.2007.02061.x](https://doi.org/10.1111/j.1755-0998.2007.02061.x)
- Waters TF (1983) Replacement of brook trout by brown trout over 15 Years in a Minnesota stream: production and abundance. *Trans Am Fish Soc* 112(2A):137–146. doi:[10.1577/1548-8659\(1983\)112%3C137:robtbb%3E2.0.co;2](https://doi.org/10.1577/1548-8659(1983)112%3C137:robtbb%3E2.0.co;2)
- Whiteley A, Hastings K, Wenburg J, Frissell C, Martin J, Allendorf F (2010) Genetic variation and effective population size in isolated populations of coastal cutthroat trout. *Conserv Genet* 11(5):1929–1943. doi:[10.1007/s10592-010-0083-y](https://doi.org/10.1007/s10592-010-0083-y)
- Wilson AJ, Hutchings JA, Ferguson MM (2004) Dispersal in a stream dwelling salmonid: Inferences from tagging and microsatellite studies. *Conserv Genet* 5(1):25–37. doi:[10.1023/b%253acoge.0000014053.97782.79](https://doi.org/10.1023/b%253acoge.0000014053.97782.79)
- Wydoski RS, Cooper EL (1966) Maturation and fecundity of brook trout from infertile streams. *J Fish Res Bd Can* 23(5):623–649. doi:[10.1139/f66-055](https://doi.org/10.1139/f66-055)
- Young MK (1994) Mobility of brown trout in south-central Wyoming streams. *Can J Zool* 72(12):2078–2083. doi:[10.1139/z94-278](https://doi.org/10.1139/z94-278)
- Young RG, Hayes JW, Hay J (2010) Movement and mortality of adult brown trout in the Motupiko River, New Zealand: effects of water temperature, flow, and flooding. *Trans Am Fish Soc* 139(1):137–146. doi:[10.1577/t08-148.1](https://doi.org/10.1577/t08-148.1)