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Transactions of the American Fisheries Society 139:000–000, 2010
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DOI: 10.1577/T10-027.1

[Article]

Dispersal and Within-Stream Spatial Population Structure of Brook Trout Revealed by Pedigree Reconstruction Analysis

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Abstract.—Spatial patterns of spawning and early dispersal have important implications for the population dynamics of stream-dwelling salmonids, but the limitations of marking technology have made it difficult to measure these processes in wild populations. We used microsatellite DNA markers and sibship and parentage analyses to follow the dispersal, spatial distribution, and distribution of reproductive success in a small, isolated north-central Virginia population of brook trout *Salvelinus fontinalis* at 4, 16, and 28 months after fry emergence. For the 2004 year-class (high-recruitment cohort), we identified 180 full-sibling families representing individual spawning events. Offspring were unevenly distributed across families, with 16% of the families accounting for 50% of the offspring and 53% of the families being represented by fewer than three individuals. However, a large proportion of adults had some successful reproduction. Spatial and family size distributions at 4 months after emergence were similar between the 2004 and 2006 (low-recruitment) year-classes in spite of a threefold difference in abundance. The spatial locations of full sibs were closely associated, indicating limited dispersal in the first 4 months postemergence. The spatial locations of assigned parents were correlated with the locations of their offspring. For the 2004 cohort, sibling dispersal substantially increased after the 4-month sample, but neither fish length, family size (number of individuals), nor fish density was related to dispersal distance at any postemergence time interval. In this study, we demonstrate the ability of sibship and parentage analyses to reveal important aspects of brook trout population structure and movement. Our results suggest that limited dispersal by age-0 brook trout and their parents results in a high level of within-stream spatial population structure even in the absence of barriers to movement, and this must be accounted for in genetic surveys and management studies.

Stream-dwelling salmonids have a characteristic reproductive mode involving egg deposition and incubation in discrete nests, or redds, in the streambed (Fleming and Reynolds 2004). When fry emerge from these redds, they disperse in search of territories that provide suitable shelter and feeding opportunities (Bujold et al. 2004; Armstrong and Nislow 2006). This life history stage has important implications for population dynamics and management because a large proportion of total mortality may occur during this stage, which can exert a strong influence on cohort strength and population abundance (Elliott 1989; Armstrong and Nislow 2006). However, particularly for wild populations, challenges in effectively marking and following young-of-the-year (age-0) salmonids as they disperse from redds have prevented us from obtaining quantitative estimates of dispersal and accurate descriptions of the resultant pattern of local (within-stream) spatial population structure. For example, a number of studies have found that spawning is limited to small areas within streams or is associated with directed migration to small tributaries (Petty and Lamothe 2005; Letcher et al. 2007), which have consequent implications for local density-dependent population dynamics (Einum et al. 2008). However, determining the spatial distribution of spawning is a major challenge for species where

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Received February 8, 2010; accepted April 9, 2010
Published online Month 00, 2010

spawning locations are difficult to observe directly. This is frequently the case for small-bodied resident trout in headwater streams.

In addition to the uncertainties regarding the spatial population distribution of reproduction, previous studies of age-0 salmonids have been inconsistent with respect to the frequency and distance of juvenile salmon dispersal. A number of studies have indicated limited dispersal from either natural (McFadden 1961; Latta 1962; Hunt and Brynildson 1964; Miller 1970) or experimental redds (Einum and Nislow 2005) months after emergence, whereas others have demonstrated extensive movements (Hunt 1965; Hunt 1974). In addition, the extent to which dispersal is density-dependent or individually size-dependent is unclear at this early stage. Small individuals at a potential competitive disadvantage may be forced to disperse further than large individuals (Bujold et al. 2004). In the process they may incur risks that may be responsible for size-selective mortality following
?1 emergence (Elliott 1989; Einum and Fleming 2000). Similarly, although fry that emerge at high densities may be expected to disperse greater distances, density-dependent dispersal has not been demonstrated for postemergence salmonid fry (Einum and Nislow 2005). Based on experimental manipulations, Einum et al. (2006) suggest that high density-dependent and size-dependent mortality just after emergence reduces the potential for similar dependence in dispersal, but this has not been assessed in wild populations. Patterns of movement and dispersal also have important implications for population assessment. Limited dispersal will result in spatial population structure both in terms of variation in local abundance (Einum and Nislow 2005) and in terms of local genetic variation (Hansen et al. 1997), which can lead to biases, if populations are sampled at inappropriate scales.

Genetic tools provide a way to assess local dispersal during early juvenile life history stages, and the use of genetics to estimate dispersal dynamics has been the subject of a recent major review (Broquet and Petit 2009). With respect to stream salmonids, Webb et al. (2001) stocked Atlantic salmon fry from known families in a Scottish stream and, upon recapture, used family affiliation to estimate dispersal distance in the first 4 months after stocking. For wild populations with unknown matings, recently developed genetic and statistical tools allow us to expand upon pedigree reconstruction methods by improving accuracy of assigned parents and assessing accuracy of reconstruct-
?2 ed pedigrees (Coombs et al. in press a, b). Because it is fair to assume an initial point source for individual families (individual redds) for small-bodied resident trout, the dispersion pattern of age-0 full siblings should give a robust estimate of early life history dispersal in wild populations. In addition to the spatial distribution these analyses yield an estimate of individual variation in successful reproduction, which is a major contributor to effective population size, particularly for small, isolated populations (Charlesworth 2009). Such populations in headwater streams represent a large proportion of the distribution of brook trout *Salvelinus fontinalis* in the eastern USA (Hudy et al. 2008). As a consequence, this species provides an excellent model for characterizing local population structure and early life history dynamics that are directly relevant for conservation and management.

In this study we characterized postemergence spatial distribution, dispersal, and population structure of a typical southern Appalachian brook trout population. We analyzed microsatellite DNA from more than 2,000 brook trout individuals, assigned individuals to family groups, and used recently developed software tools to improve and assess pedigree accuracy. Specific objectives were to (1) evaluate the number, spatial distribution, and relative contribution of full-sibling families, (2) test the effects of body size and population density on among-family differences in dispersal, and (3) test for differences in dispersal between main-stem and tributary locations.

Methods

Study area.—The Fridley Gap watershed (560 ha), located in Rockingham County in north-central Virginia (Figure 1), is a typical southern Appalachian brook trout watershed (Hudy et al. 2008). Specific geology and land use history are summarized in Hudy et al. (2000). Fish-bearing habitat in the main stem is 1,800 m long and has an average low-flow wetted width of 3.8 m. A small fish-bearing tributary (250 m long; average low-flow wetted width, 1.8 m) enters the main stem at 1,500 m upstream of the downstream fish-bearing border (dam in Figure 1). The upstream limit of brook trout distribution is set by intermittent flows in the headwaters, and the downstream extent is set by a small dam, impassable to both adult and young. The habitat below the dam is impacted by agricultural practices that have severely degraded riparian habitat making it no longer suitable for brook trout. The nearest source population of brook trout is more than 85 stream km downstream.

Brook trout sampling.—We used one-pass electrofishing to census the entire Fridley Gap subwatershed (about 2 km of stream) during July 2004, 2005, and 2006. We recorded location (nearest upstream meter) and collected fin clips from all brook trout captured (Figure 1). We sampled every July because that was the time when age-0 brook trout become large enough to

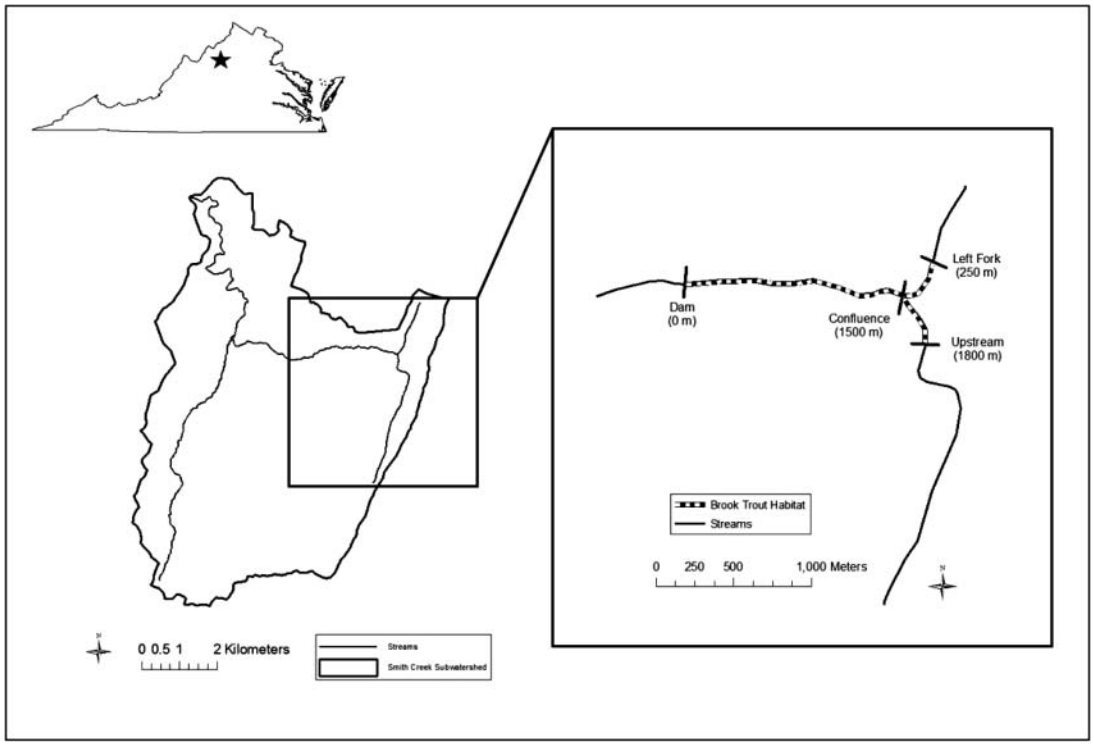

FIGURE 1.—Location of the Fridley Gap brook trout habitat patch within the Smith Creek subwatershed. The dam represents the downstream terminus of brook trout habitat (0 m). The upstream limit of brook trout habitat occurs 1,800 m from the dam. The Left Fork tributary provides an additional 250 m of fish-bearing habitat upstream of the confluence with Smith Creek.

be efficiently captured by electrofishing. Single-pass electrofishing was significantly correlated with mark–recapture population estimates in this watershed for both age-0 (<100 mm total length in July; $r = 0.87$) and age-2 (>16 months postemergence; >100 mm total length in July; $r = 0.91$) brook trout (Hudy et al. 2000). The Fridley gap site, to date, has been the subject of a long-term study employing the same sampling protocol since 1993.

Genetic analysis and pedigree reconstruction.—Genetic data were used to (1) assign individual age-0 brook trout into full-sibling families, (2) assign individuals as parents to these families, and (3) uniquely identify individuals. Our analysis also revealed half-sib family structure, but because half-sibling families provided no additional information on spatial distribution and dispersal, they were not considered further for these analyses. To accurately meet the above objectives (based upon simulation results below that were parameterized using allele frequencies from screened loci), we selected a panel of eight microsatellite loci: *SfoC-113*, *SfoD-75*, *SfoC-88*, *SfoD-100*, *SfoC-115*, *SfoC-129*, *SfoC-24* (King et al. 2003), and *SsaD-237* (King et al. 2005) . Protocols for DNA extraction and amplification followed King et al. (2005). Loci were electrophoresed on an ABI Prism 3100-Avant genetic analyzer (Applied Biosystems Inc., Foster City, California), and alleles were scored using GENEMAPPER version 3.2 and PEAK SCANNER version 1.0 software (Applied Biosystems Inc.). Allele number and observed and expected heterozygosities were calculated using GDA v1.0 (Lewis and Zaykin 2001). Estimation of f_{is}, an analog of Wright's genetic differentiation index (F_{IS}), and testing for departures from Hardy–Weinberg equilibrium were performed using GENEPOP v4.0.10 (Rousset 2008). Testing was conducted using the heterozygote deficiency option because the presence of a null allele was suspected for at least one locus. Tests were performed for each locus in each population ($k = 24$), and significance was assessed using a sequential Bonferroni correction (Holm 1979; Rice 1989) with $\alpha = 0.05$. For significant loci, null allele frequencies were estimated using ML-Relate version 090408 (Kalinowski et al. 2006).

The power of the loci panel to accurately reconstruct full-sibling families and assign parents was assessed

using simulated data generated by the program PEDAGOG v1.2 (Coombs et al., in press a). Simulations consisted of generating a population with genetic (allele number, heterozygosity, and null allele frequencies) and demographic attributes similar to those of the Fridley Gap brook trout population and subjecting it to a yearly sampling scheme. A total of 10 replicates were simulated. Sibship reconstruction and initial parentage assignment analyses were performed on the simulated output using the programs COLONY version 1.2 (Wang 2004) for sibship and PEDAPP version 1.1 (Almudevar 2007) for parentage. Final parentage assignments were acquired using the sibship constraint method within the program PEDAGREE version 1.04 (Coombs et al., in press b). Accuracies of sibship reconstruction and parentage assignment output for simulated data were calculated using PEDAGREE.

Analyses for three different sibship groupings were performed on the Fridley Gap data set using the same pedigree reconstruction methods detailed above. The first two analyses restricted sibship groups to age-0 fish captured during the 2004 and 2006 samples. This allowed for comparison of family distributions and dispersal distances for age-0 to age-2 trout. The third analysis supplemented age-0 fish captured during the 2004 sample with age-1 and age-2 fish from this same cohort captured during the 2005 and 2006 samples. Individuals deemed to be genetic recaptures were removed prior to analysis to eliminate family size inflation. Output from this analysis was used to assess family dispersal over time.

Assessment of the power of the loci panel to genetically identify recaptured individuals to assess movement between samples was determined by calculating observed probability of identity (P_{ID}) values (Waits et al. 2001). In essence, P_{ID} equals the likelihood that any two individuals in the population will share identical genotypes and thus be indistinguishable from one another. All P_{ID} values were calculated for each sample separately to avoid bias caused by individuals captured in multiple samples. As an additional test of the loci panel's power, a subset of the population (blind to the genetic analysis) was implanted with passive integrated transponder (PIT) tags (Biomark, Boise, Idaho), allowing for direct evaluation of individual identification accuracy.

Dispersal, growth, and relative abundance.—We characterized dispersal, body size, and relative abundance for full-sibling families from the 2004 year-class at 4, 16, and 28 months postemergence and for the 2006 year-class at 4 months only. We did not collect DNA data from age-0 fish of the 2005 year-class. Time since emergence is an approximation based on previous observations (Hudy, personal observation). Redd locations were rarely visually identifiable in this watershed before, during, or after spawning activity. Consequently, we used the centroid location (center of the linear spatial distribution of the family along the stream) of each full-sibling family during our first sampling (4 months postemergence, July 2004) as the approximate redd location (inferred redd) to determine dispersal metrics. We defined dispersal of an individual brook trout as the distance between its capture location and its family's inferred redd location. We also measured total length of all fish captured and calculated abundance of brook trout by 50-m stream lengths to determine potential density-dependent and size-dependent effects on dispersal. The relative change in abundance of each full-sibling family after 16 and 28 months was used as a proxy for survival.

Statistical analysis.—We used analysis of variance (ANOVA) to test for significant differences among full-sibling families and years for dispersal and growth metrics, and we used Tukey's test for multiple comparisons. We used *t*-tests to compare differences between two means or between 2 years. If data were not normally distributed and could not be appropriately transformed, we used nonparametric methods (Kruskal–Wallis ANOVA on ranks with the Dunn's method for multiple comparison procedures or Mann–Whitney *U*-tests; Sokal and Rohlf 1995). We used Spearman's rank correlation coefficient to determine whether families that contained more or larger individuals were more likely to have higher dispersal distances. Statistical significance for all tests was set at $\alpha = 0.05$. Because many full-sibling families were represented by only a few individuals, we limited statistical analyses of among-family and among-year differences in size and dispersal to those full-sibling families where the sample size was 3 or more (main stem = 73 families; tributary = 11 families) for the 2004 year-class sampled in 2004 versus 10 main-stem families and 7 tributary families for the 2004 year-class sampled in 2005 and 2006. We used the same 10 full-sibling main-stem families and 7 full-sibling tributary families from the 2004 year-class when displaying or analyzing patterns of dispersal after 4,16, and 28 months. To determine the frequency distribution of individuals across families we used all assigned families, including those with more than three individuals.

Results

General Characteristics of the Brook Trout Population

One-pass sampling of the population netted 838 age 0s and 382 adults in 2004, 233 age-0s and 416 adults (248 from the 2004 year-class) in 2005, and 103 age 0s and 447 adults (243 from 2004 year-class) in 2006. The 2004 year-class was the largest year-class on record

TABLE 1.—Single-locus summary statistics for adult (age-1 and older) brook trout captured in Fridley Gap during 2004, 2005, and 2006. Measures as follows are: number of individuals genotyped (N_G), observed number of alleles (A_O), observed heterozygosity (H_O), expected heterozygosity (H_E), an analogue of Wright's F_{IS} statistic (f_{is}), and probability of departure from Hardy–Weinberg expectations in the direction of heterozygote deficiency (phonetic)). *P*-values in bold italics indicate significant departures from expected Hardy–Weinberg equilibrium when evaluated using a sequential Bonferroni correction for multiple tests ($k = 24$, $\alpha = 0.05$).

	SfoC-113	SfoD-75	SfoC-88	SfoD-100	SfoC-115	SfoC-129	SfoC-24	SsaD-237	Average
					2004				
N_G	382	382	382	382	382	382	382	361	379.375
A_O	10	12	8	11	18	5	6	20	11.250
H_O	0.801	0.819	0.764	0.859	0.793	0.654	0.791	0.429	0.739
H_E	0.778	0.841	0.750	0.845	0.837	0.677	0.751	0.872	0.794
f_{is}	−0.030	0.026	−0.019	−0.017	0.052	0.033	−0.053	0.508	0.063
P	0.990	0.351	0.667	0.655	0.151	0.053	0.926	***0.000***	
					2005				
N_G	304	304	304	304	304	304	304	293	302.625
A_O	10	11	7	11	17	4	6	18	10.500
H_O	0.832	0.842	0.776	0.895	0.845	0.641	0.704	0.406	0.743
H_E	0.801	0.836	0.749	0.851	0.846	0.631	0.735	0.874	0.790
f_{is}	−0.039	−0.008	−0.037	−0.052	0.001	−0.017	0.042	0.536	0.053
P	0.991	0.648	0.892	0.970	0.221	0.606	0.288	***0.000***	
					2006				
N_G	447	447	447	447	447	447	447	418	443.375
A_O	10	11	7	11	17	4	6	19	10.625
H_O	0.776	0.792	0.729	0.881	0.859	0.678	0.716	0.416	0.731
H_E	0.782	0.827	0.757	0.859	0.858	0.655	0.737	0.861	0.792
f_{is}	0.007	0.042	0.036	−0.026	−0.001	−0.035	0.029	0.516	0.071
P	0.195	0.060	0.359	0.897	0.328	0.704	0.097	***0.000***	

over the 15-year monitoring period of this population (1994–2009), three times the long-term average and two times the second-highest year-class (average year-class = 268, range 22–813). In contrast, the 2006 year-class was one of the smallest recorded. The adult population in 2004 was near the 15-year average (average adult relative abundance = 304, range 121–531). The 2004 year-class averaged 64 mm in total length (SD = 8.2, range 42–90 mm) at 4 months postemergence, 118 mm (12.5, 89–149 mm) at 16 months postemergence, and 148 mm (25.4, 114–213 mm) at 28 months postemergence.

Genetic Analysis and Pedigree Reconstruction

A total of 2,379 individuals captured during the 2004, 2005, and 2006 samples were genotyped. Loci summary statistics for individual adults (>age 1) grouped by sample year are shown in Table 1. Heterozygote deficiency tests resulted in significant departures from Hardy–Weinberg equilibrium for the *SsaD-237* locus in all three samples. Null allele frequencies were estimated to be 0.288 (2004), 0.282 (2005), and 0.300 (2006). The weighted average (0.291) of these three frequency estimates was used to parameterize simulations for pedigree reconstruction accuracy assessment.

Sibship reconstruction and parentage assignment analyses performed on the simulated data sets both indicated a high degree of power to accurately reconstruct full-sibling families and assign parents. For reconstructed full-sibling families composed of at least three individuals, inferred families had a correct partition rate of 95.2% (SE, 0.7), and assigned parents had an accuracy of 93.1% (SE, 0.9). Accuracies for both methods improved as reconstructed full-sibling family size increased. For example, reconstructed full-sibling families composed of at least 10 individuals resulted in accuracies of 98.6% (SE, 0.1) for sibship and 97.1% (SE, 1.2) for parentage.

Observed P_{ID} values indicated that the loci panel was also able to resolve the identity of individuals with a high degree of accuracy. Averaged over the three samples, the observed P_{ID} value was 6.43^{-6}. This is equivalent to two individuals having identical genotypes once out of all pair-wise comparisons among 558 individuals (155,503 comparisons). The blind PIT tag study provided further support for the ability of the loci panel to resolve individual identity. A total of 74 PIT-tagged individuals were recaptured during a subsequent sample. Of these, 71 (96%) were correctly identified as the same individual, based on matching genotypes. Two of the three misidentifications resulted from field data-entry errors, which were discovered because the genotype matched a different individual. The third error was from a miscalled allele, which led to the two genotypes differing by a single allele. The per-allele

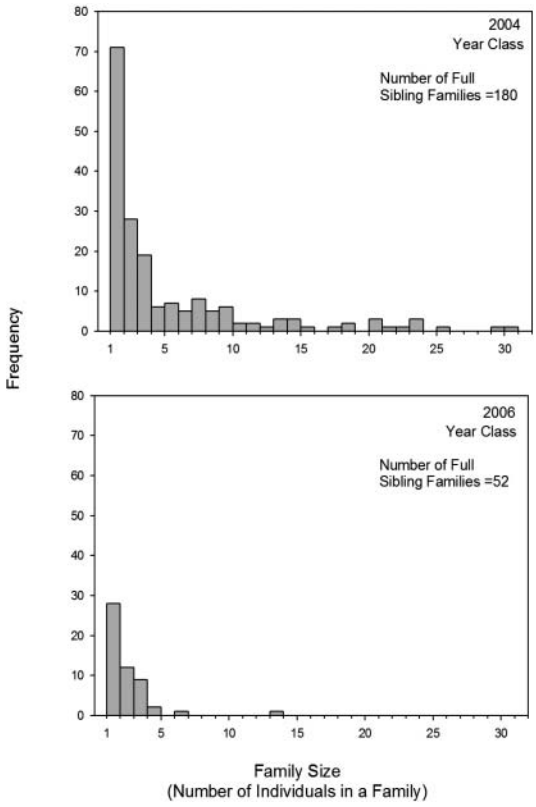

FIGURE 2.—Frequency distributions of brook trout family size for the strong 2004 year-class and the weak 2006 year-class at 4 months postemergence. The bars indicate the numbers of individuals in a full-sibling family (e.g., in the 2004 year-class, there were 71 full-sibling families with only 1 individual and 1 family with 31 individuals).

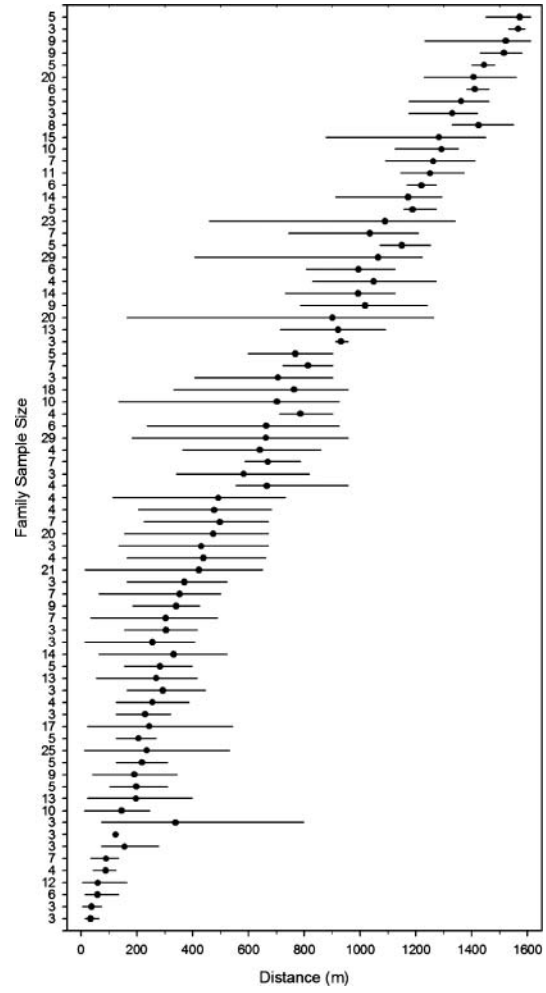

FIGURE 3.—Dispersal patterns and inferred redd locations (centroids) of full-sibling brook trout families within the mainstem study site location (2004 year-class; only full-sibling families with three or more individuals). Each black dot represents an inferred redd location, the accompanying horizontal line the range of dispersal distances (see Figure 1) from that location at 4 months postemergence. The *y*-axis shows the number of individuals within each full-sibling family.

genotyping error rate for the 74 PIT-tagged individuals was 1/1,184 (0.08%).

Sibship reconstruction revealed a large number of full-sibling families, which probably resulted from individual spawning events. In the 2004 sample a total of 838 age 0s were reconstructed into 180 full-sibling families (main stem = 165, tributary = 15). In the 2006 sample a substantially smaller total of 103 age 0s were reconstructed into 52 full-sibling families (main stem = 44, tributary = 8). In both years family representation was skewed, 16% of the families accounting for 50% of the offspring in 2004 and 25% of the families accounting for 51% of the offspring in 2006 (Figure 2). However, in both years a large percentage of reconstructed families (53% in 2004, 75% in 2006) were composed of only one or two siblings. For age 0s captured during the 2004 sample, supplemented with age-1 and older fish captured during the 2005 and 2006 samples, a total of 115 full-sibling families (1,082 individuals) were retained after filtering (for families containing a minimum of three individuals). Parentage analysis performed on these families assigned a total of 95 parents to 73 families (22 families with both parents assigned).

Inferred Redd Distribution and Offspring Dispersion

Based on the distribution of 2004 year-class full-sibling families, redds were distributed throughout the

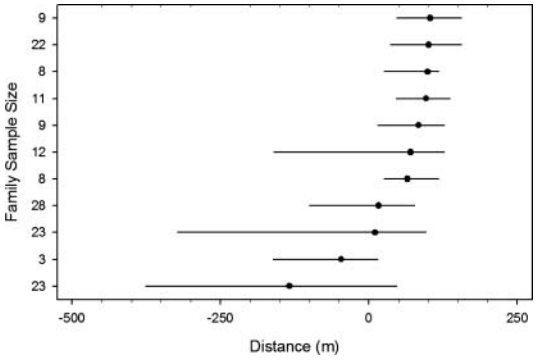

FIGURE 4.—Dispersal patterns and inferred redd locations of full-sibling brook trout families within the tributary study site location. Negative numbers indicate dispersal downstream into the main stem; see Figure 3 for more details.

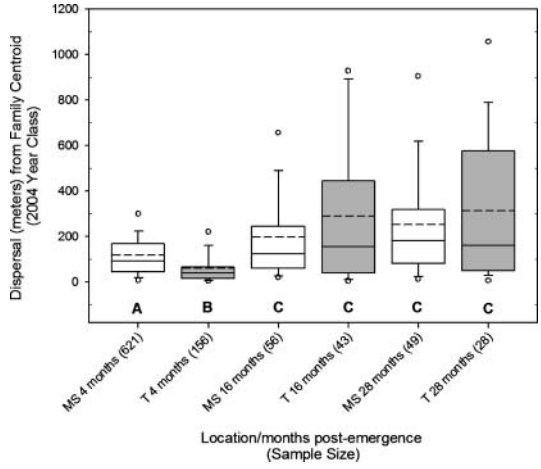

FIGURE 5.—Box plots of the dispersal distances of the 2004 year-class categorized by emergence in the main-stem (MS) or tributary (T) location at three postemergence sample times: 4 months (July 2004), 16 months (July 2005), and 28 months (July 2006). The solid line represents the median dispersal for each group and the dotted line the average dispersal; sample sizes (total number of individuals) are given in parentheses. Each box represents 50% of all values, the whiskers represent the first and third quartiles, and the white circles represent outliers. Box plots with the same letter are not significantly different ($P > 0.05$).

subwatershed (Figures 3, 4). In July 2004, 7 months after peak spawning time and 4 months postemergence, the parent locations were closely associated with the approximated redd locations both in the main stem (average distance from family centroid = 193 m, SD = 150, median = 142, $N = 69$) and tributary (average distance = 117 m, SD = 171, median = 61, $N = 13$). The majority of parents were located upstream of the inferred redd location (main stem = 81%, tributary = 77%).

Full-sibling families were highly clumped 4 months postemergence, and the mean dispersal in the main stem (109 m) was significantly higher than the tributary (52 m; ANOVA: $F_{952} = 40.552$, $P < 0.001$) (Figure 5). Dispersal from the original inferred redd locations increased substantially over time. After 16 months, mean dispersal increased both within the main stem (197 m) and tributary (289 m); however, there were no longer significant differences between the two locations (Figure 5). Mean dispersal at 28 months postemergence (main stem, 253 m; tributary, 313 m) was not significantly different from dispersal after 16 months or by location (Figure 5). Individual families usually, but not always, dispersed further downstream through time (Figures 6, 7), and a large portion of the 2004 year-class that emerged in the tributary dispersed downstream into the main stem after 16–28 months (Figure 7). Main-stem dispersion of age 0s of the 2006 year-class at 4 months after emergence (179 m, SD = 118) was significantly greater ($t = -3.765$, df = 650, $P < 0.001$) than observed dispersion of age 0s of the 2004 year-class (109 m, SD = 99). However, age-0 dispersion in the tributary did not differ significantly among year-classes ($t = 0.970$, df = 176, $P = 0.333$).

There was no difference in body length between main stem and tributary brook trout at 4 months ($t = 0.367$, df = 325, $P = 0.714$). Variation in dispersal was generally not explained by individual body length. At 4 months postemergence an individual brook trout's length was not correlated (linear regression) with dispersal distance from its inferred redd location for fish spawned in either the main stem (df = 620, $r^2 = 0.001$, $P > 0.05$) or the tributary (df = 155, $r^2 = 0.018$, $P > 0.05$). At 16 months postemergence (July 2005), larger fish in the main stem (df = 55, $r^2 = 0.051$, $P < 0.001$) and tributary (df = 42, $r^2 = 0.035$, $P < 0.001$) had slightly greater dispersal distances from their inferred redd location, but explanatory power was low. Similarly, fish length and dispersal were weakly correlated 28 months postemergence both in the main stem (df = 30, $r^2 = 0.094$, $P < 0.001$) and tributary (df = 21, $r^2 < 0.076$, $P < 0.001$).

Full-Sibling Relative Abundance

Based on Spearman's rank correlation coefficient, the 2004 year-class full-sibling families with high abundance ranks after 4 months were more likely to have high abundance ranks at 16 months postemergence (2005 sample: $N = 17$, $r_s = 0.498$, $P > 0.05$), but these ranks were not maintained at 28 months (2006 sample: $N = 17$, $r_s = 0.325$, $P < 0.01$). The rankings of 2004 year-class full-sibling families relative abundance

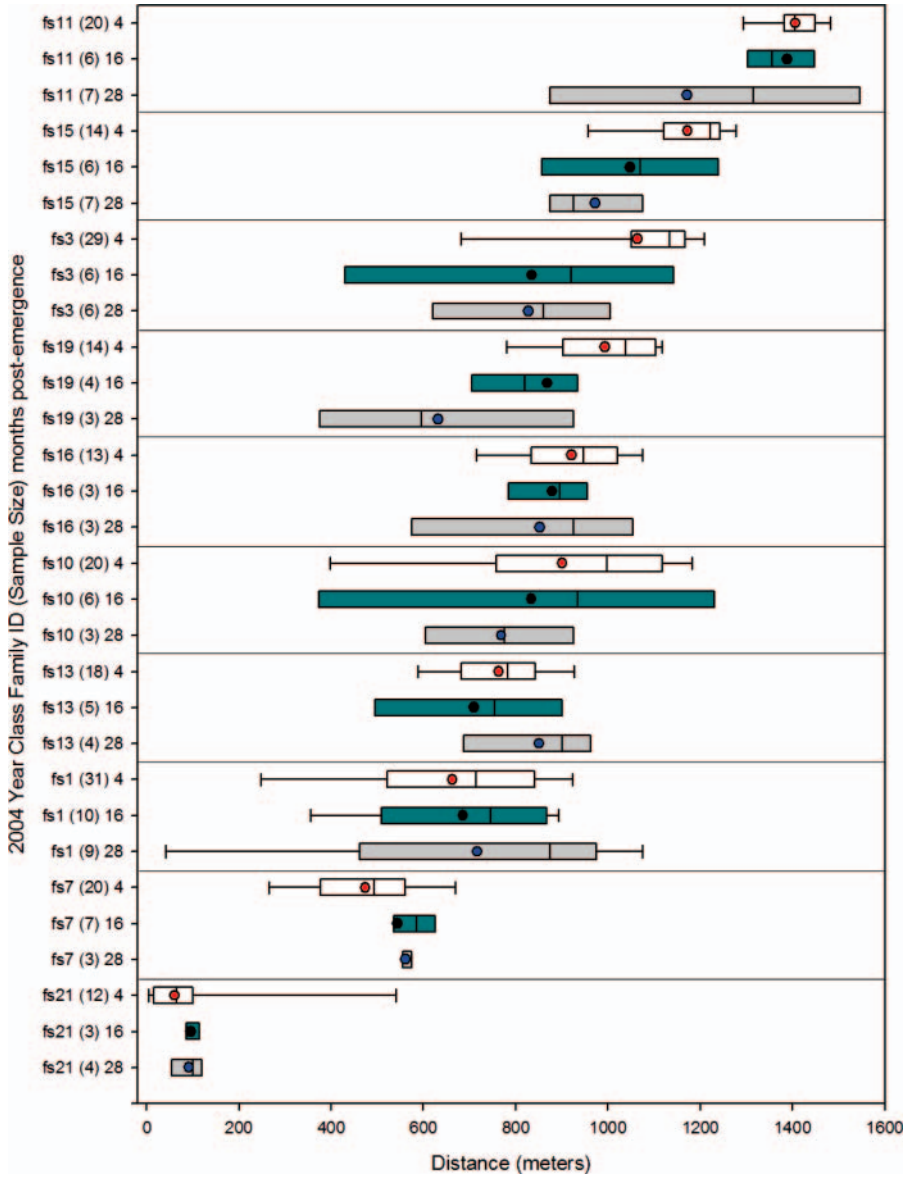

FIGURE 6.—Box plots of the dispersal patterns of individual full-sibling brook trout families (2004 year-class; only full-sibling families with three or more individuals) over three postemergence sample times: 4 months (July 2004; white), 16 months (July 2005; blue), and 28 months (July 2006; gray). The colored circles represent the mean dispersal, the solid black lines the median dispersal. The box represents 50% of all values, the whiskers (if present) the first and third quartiles; the colored circle for the 2004 sample period is also the inferred redd location for each full-sibling family. The *y*-axis shows the 2004 year-class full-sibling (fs) family identification number, the sample size (in parentheses), and the sample period in months postemergence (4, 16, or 28).

were not correlated with the rankings of family length at 4 months (2004 sample: $N = 17$, $r_s = 0.211$, $P > 0.05$), 16 months (2005 sample: $N = 17$, $r_s = -0.104$, $P > 0.05$), or 28 months (2006 sample: $N = 17$, $r_s = -0.051$, $P > 0.05$).

Discussion

Using genetically reconstructed pedigrees we were able to describe the spatial distribution of spawning sites, dispersal from these sites, and the distribution of individuals across families in a wild headwater brook

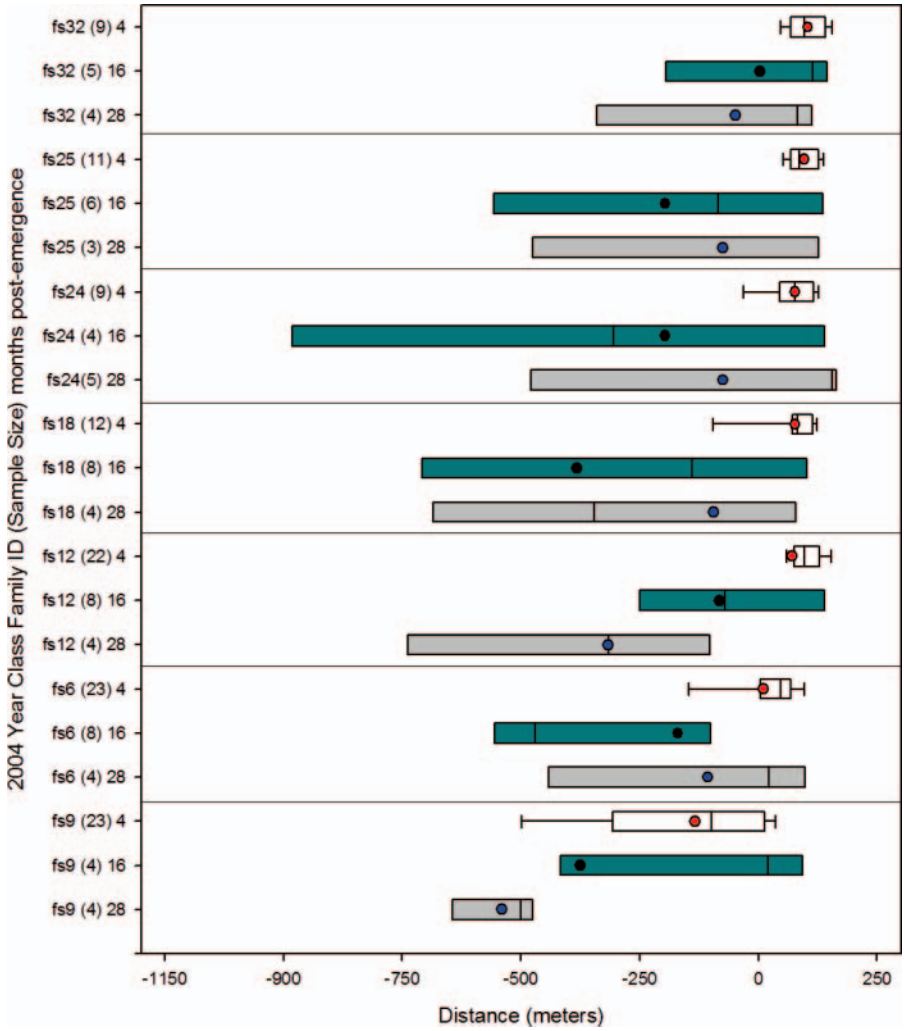

FIGURE 7.—Box plots of the dispersal patterns of individual full-sibling brook trout families (2004 year-class; only full-sibling families with three or more individuals) over three postemergence sample periods. Negative numbers indicate dispersal downstream into the main stem. See Figure 6 for more details.

trout population. Although conservation genetics techniques have been previously used to estimate aspects of dispersal (Broquet and Petit 2009), our use of sibship and parentage analysis allowed us to estimate juvenile dispersal at local within-population scales that are difficult if not impossible to accomplish using other techniques. This is an important advance given the influence of these mechanisms in stream salmonid population dynamics. In addition, these advances surmount some of the difficulties in tagging and tracking individuals during early life history and in visual identification of spawning locations. In this headwater stream, our results suggest that limited dispersal by age-0 brook trout and their parents results in a high level of spatial population structure, even in the absence of obvious physical barriers to movement. This spatial structure was not apparent after 16 months postemergence due to greater dispersal of older fish. Based on the spatial distribution of age-0 families, it appears that spawning occurs throughout the study system (about 2.0 km). The number of full-sibling families indicated that a relatively large proportion of the adult population produced offspring that survived until the first sampling period. We were able to obtain this information via a standard one-pass electrofishing census typically used in southern Appalachian brook trout streams. This points to the utility of our approach for resolving detailed spatial population structure of

resident stream fish populations and to do such with reasonable amounts of sampling and analytical effort.

The limited dispersal observed for age-0 fish in our study is consistent with the few earlier studies of other salmonid species. In Lawrence Creek, Michigan, Hunt and Brynildson (1964) and Miller (1970) found that downstream migration of age-0 brook trout before June was negligible and that direct density dependent interactions among fry were not the underlying cause of the dispersal among the 1.5-km study stations. However, lack of information on specific redd locations makes it impossible to estimate finer scale dispersal (<1.5 km) from these data. Similarly, Einum and Nislow (2005), who outplanted eggs of Atlantic salmon *Salmo salar* at 150-m intervals in Norwegian streams, found that age-0 fish were highly clumped around nest locations when sampled 3 months after emergence. As in our study, individual size and local density were unrelated to early dispersal, and limited dispersal from nests occurred in both high-recruitment and low-recruitment years. Our study also found that dispersal increased after the 4-month sample, which is consistent with the results of Hunt (1965) for wild brook trout in Lawrence Creek. Similarly, Einum et al. (2006) found that dispersal was significantly greater for older juvenile Atlantic salmon than it was for younger fish, as well as being significantly size-dependent and density-dependent.

The spatial association between parents and their offspring revealed by parentage analysis was an unexpected result of the study because fish sampling occurred nearly 7 months after spawning. This spatial association reinforced our use of the centroid of the family spatial distribution at 4 months after emergence as an approximation of initial redd location. Because parents were generally located slightly upstream of the centroid of the family distribution, our inferred redd locations may have had a slight downstream bias. We did not feel confident, however in adjusting inferred redd locations based on parent locations and maintain that the use of the center of the offspring distribution represents the most reasonable approximation. In addition, we assigned very few main-stem parents to tributary families, suggesting a lack of spawning movement from main stem to tributary sections in the interim between spawning and sampling. This is in contrast to previous studies, which have observed extensive and frequent spawning movements into tributaries and returning to main stems in stream-dwelling brook trout (Petty and Lamothe 2005; Letcher et al. 2007). Finally, our results support the previously made observation that while some individuals in some brook trout populations may make extensive movements (Gowan et al. 1994), a large proportion of brook trout in other systems appear to be highly site-attached (Rodríguez 2002). For brook trout in the southern Appalachian portion of their range, where most populations currently occur in small patches of stream habitat, a highly sedentary strategy could be favored for most individuals because of limited upstream (due to low flows) and downstream (due to high temperatures and the presence of predators and competitors) habitats.

The distribution of reproductive success across individuals and families within a population has major conservation implications. In Fridley Gap, the distribution of the number of age-0 offspring among families was somewhat skewed in both a high-recruitment (2004) and low-recruitment (2006) year. Overall, however, relative to the size of the adult population, offspring were distributed over a large number of families. A large proportion of successful spawners were represented by less than three age-0 offspring at 4 months after emergence, and no families had extremely large numbers of age-0 offspring (maximum family size = 32 in the 2004 cohort). Further, relative abundance ranks of families did not persist from 4 months to 28 months after emergence, increasing the overall evenness of the distribution of individuals among families. In small, isolated populations that are characteristic of the southern Appalachian distribution of brook trout, having a large proportion of adults participating in reproduction may be critical to reducing stochastic extinction risk and the loss of genetic diversity. We suggest that future research should test the generality of this observation across multiple populations in brook trout and other headwater species. At the same time, the strong within-stream spatial population structure and limited dispersal we observed underscores the importance of conducting genetic surveys at appropriate spatial scales. In such cases, spatially limited surveys will underestimate genetic diversity and gene flow (Hansen et al. 1997).

In addition to these major findings our results have other important management implications. Our analyses were able to correctly identify unique individuals with a very high degree of accuracy, suggesting the use of genetic identification as a primary or secondary tag for standard management applications. For example, in related studies within the Fridley Gap watershed, these genetic tags were used to validate age and growth, detect movement and determine PIT tag losses. In addition, the ability to individually identify large numbers of postemergent salmonid fry makes it possible to accurately measure individual growth and survival at this critical life history stage. Lack of this information has been a major constraint on our ability

to assess the determinants of early survival and growth (Armstrong and Nislow 2006). The patterns of spatial dispersion may also provide critical management information. For example, inferred redd locations can provide information on the suitability and spatial distribution of spawning habitats when redds are difficult to directly observe, which is often the case in small headwater streams. Further, the occurrence of members of the same family on different sides of a potential or former barrier provides unambiguous evidence of passage without the limitations and cost of traditional tagging studies. As the cost of genetic samples decreases and the applicability of genetics software continues to broaden these techniques should become more cost-effective and useful for a wide range of applications.

Acknowledgments

The following organizations provided financial assistance or volunteer support: James Madison University, George Washington and Jefferson National Forest; Virginia Department of Game and Inland Fisheries; U.S. Forest Service, Northern Research Station; and U.S. Geological Survey, Leetown Science Center; and Conte Anadromous Fish Research Laboratory. The authors are appreciative of the help of the following individuals: Seth Coffman, Jeremy Shiflet, Morgan McHugh, Brad Fink, Sara Sweeten, Keith Whalen, Teresa Thieling, Chas Kyger, Brad Trumbo, and Gonzalo Mendez.

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