

Spatial and Seasonal Dynamics of Brook Trout Populations Inhabiting a Central Appalachian Watershed

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Abstract.—We quantified the watershed-scale spatial population dynamics of brook trout *Salvelinus fontinalis* in the Second Fork, a third-order tributary of Shavers Fork in eastern West Virginia. We used visual surveys, electrofishing, and mark–recapture techniques to quantify brook trout spawning intensity, population density, size structure, and demographic rates (apparent survival and immigration) throughout the watershed. Our analyses produced the following results. Spawning by brook trout was concentrated in streams with small basin areas (i.e., segments draining less than 3 km²), relatively high alkalinity (>10 mg CaCO₃/L), and high amounts of instream cover. The spatial distribution of juvenile and small-adult brook trout within the watershed was relatively stable and was significantly correlated with spawning intensity. However, no such relationship was observed for large adults, which exhibited highly variable distribution patterns related to seasonally important habitat features, including instream cover, stream depth and width, and riparian canopy cover. Brook trout survival and immigration rates varied seasonally, spatially, and among size-classes. Differential survival and immigration tended to concentrate juveniles and small adults in small, alkaline streams, whereas dispersal tended to redistribute large adults at the watershed scale. Our results suggest that spatial and temporal variations in spawning, survival, and movement interact to determine the distribution, abundance, and size structure of brook trout populations at a watershed scale. These results underscore the importance of small tributaries for the persistence of brook trout in this watershed and the need to consider watershed-scale processes when designing management plans for Appalachian brook trout populations.

Populations of brook trout *Salvelinus fontinalis* within the central and southern Appalachian Mountains have suffered reductions in numbers and range due to a combination of factors, including high harvest rates, physical habitat and water quality degradation, and introduction of nonnative salmonids (Larson and Moore 1985; Flebbe 1994; Marschall and Crowder 1996; Galbreath et al. 2001). Most notable in the central Appalachian region is the negative effect of acid precipitation (Wigington et al. 1996). In West Virginia alone, an estimated 25% of all streams are impaired because of a high rate of acid deposition coupled with a poorly buffered, sandstone-dominated geology (Sharpe et al. 1987; Welsh and Perry 1997; Clayton et al. 1998).

The upper Shavers Fork watershed, located in the central Appalachian Mountains of eastern West Virginia, provides a good example of the problems confronting brook trout populations in this region. Historically (prior to 1910), this watershed possessed an extremely productive brook trout fishery. The watershed was almost completely covered in red spruce *Picea rubens* and was drained by a network of pristine coldwater streams. Currently, however, numerous factors combine to limit the productivity of the brook trout fishery. Acid precipitation has depleted the buffering capacity in many streams such that they cannot support trout reproduction and are inhabited by only a few acidophilic invertebrate taxa (Clayton et al. 1998; Bopp 2002). Sedimentation from numerous diffuse sources, such as a network of gravel roads and a ski resort, also contributes to poor water quality. In addition, a century of intensive timber harvest in the watershed, coupled with several severe floods, has dramatically altered the condition of riparian habitats and instream structural complexity, especially in the main stem of the Shavers Fork (Petty et al. 2003).

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TABLE 1.—Summary characteristics of 11 sample sites within the Second Fork watershed, West Virginia. Sites were selected to cover a range of stream size, canopy cover, temperature, and water chemistry. Average pH was calculated by converting the average concentration of H⁺ ions back to pH (standard units).

Site	Basin area (km ²)	Wetted width (m)	Average depth (m)	Canopy cover (%)	Mean July temp. (°C)	Average pH	Alkalinity (mg CaCO ₃ /L)
1	15.19	7.5	0.30	60	13.5	6.4	8.9
2	12.03	6.5	0.33	35	14.1	6.3	8.4
3	11.52	5.5	0.40	50	13.2	6.2	6.6
4	10.09	5.7	0.40	85	12.5	6.6	10.1
5	8.01	5.0	0.38	65	12.7	6.5	9.7
6	1.50	3.0	0.20	70	12.1	6.7	17.2
7	5.25	5.3	0.25	75	12.5	6.2	7.6
8	2.50	4.0	0.30	75	12.2	6.6	16.2
9	1.25	2.3	0.28	85	12.7	5.8	5.3
10	0.75	3.0	0.25	15	13.2	6.9	22.4
11	4.25	5.7	0.38	75	12.8	5.6	4.2

There is a growing interest in recovering brook trout populations to historic levels due to the potential value of restored native trout populations in this region. Effective management of these populations, however, will require a watershed-scale perspective. One reason for this is that factors currently limiting brook trout populations are spread diffusely throughout the watershed. Consequently, identification of areas critical to population productivity is needed to focus recovery efforts. A second reason is the importance of landscape-scale processes to the ecology of stream fishes (Fausch et al. 2002). It is increasingly apparent that stream habitats must be viewed as linked networks rather than independent stream reaches. In fact, an emerging paradigm in stream fish ecology views stream ecosystems as dynamic landscapes where fish movement, habitat patchiness, and life-stage-dependent shifts in critical habitat attributes interact to influence fish populations and communities at the watershed scale (Schlosser 1991;

Schlosser and Angermeier 1995; Fausch et al. 2002). For example, both Schlosser (1995) and Snodgrass and Meffe (1998) demonstrated that specific areas within a drainage network serve as sources of individuals for other areas and therefore determine patterns of fish assemblage structure at the watershed scale. Similarly, Dunham et al. (1997) demonstrated that the persistence of Lanthan cutthroat trout *Oncorhynchus clarkii henshawii* is dependent on the dispersal of individuals among geographically isolated stream reaches within drainage networks.

If similar processes influence brook trout populations in the Appalachian region, then this may have important implications for how we manage these watersheds. For example, it would influence where we focus stream remediation efforts and how we combine management actions designed to reduce fishing pressure and restore habitat and water quality within the same watershed. Consequently, our studies in the upper Shavers Fork wa-

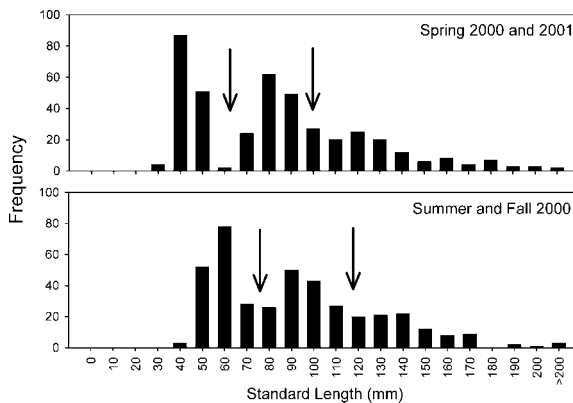


FIGURE 1.—Length-frequency histograms used during each season to classify all brook trout captured from the Second Fork watershed, West Virginia, into one of three age-classes: juveniles, small adults, and large adults.

TABLE 2.—Models used to estimate electrofishing capture probability (p), apparent survival (ϕ), and immigration (Γ) of brook trout in study segments of the Second Fork watershed, West Virginia. A combination of closed and open population estimators were used to estimate population parameters in the program MARK. Juvenile ϕ was estimated for two seasonal intervals only (summer–fall 2000; fall 2000–spring 2001), because fish could not be uniquely marked in spring. Juvenile Γ was quantified fish only for summer–fall 2000. Akaike’s information criterion (AIC_c) corrected for small-sample bias.

Model	AIC_c	Number of parameters	Description
Juveniles			
p (season \times site)	-1,407	44	Juvenile capture probability varies by season and site.
ϕ (season \times site)	224	23	Juvenile survival varies by season and site.
Γ (site)	198	12	Juvenile immigration rate varies by site.
Small adults			
p (season \times site)	-1,495	44	Small-adult capture probability varies by season and site.
ϕ (season \times site)	790	34	Small-adult survival varies by season and site.
Γ (season \times site)	782	34	Small-adult immigration rate varies by season and site.
Large adults			
p (season \times site)	-1,088	44	Large-adult capture probability varies by season and site.
ϕ (season \times site)	394	34	Large-adult survival varies by season and site.
Γ (season \times site)	339	34	Large-adult immigration rate varies by season and site.

tershed have adopted the “dynamic riverscape” view described by Fausch et al. (2002). We recognize that Appalachian watersheds exhibit a high degree of spatial and temporal complexity. We further recognize that it may be necessary for brook trout to move throughout a drainage network to access resources distributed in different areas of a watershed.

The specific objectives of our study were to (1) identify critical spawning areas for brook trout and quantify the physical and chemical factors that influence brook trout spawning intensity and juvenile recruitment within the watershed, (2) determine the extent to which spawning and recruitment

processes influence the distribution of juveniles and adults, and (3) examine how postreproductive demographic processes (i.e., survival and dispersal) interact to determine the spatial structure of brook trout populations at the watershed scale.

Study Area

Our study was conducted within the Second Fork, a third-order tributary of the upper Shavers Fork of the Cheat River, located in the Monongahela River basin. The Second Fork watershed is part of the Monongahela National Forest and comprises a mixed deciduous–coniferous forest. The Second Fork drains an area of approximately 16 km² and flows 7.5 km from its headwaters at Bald Knob (elevation = 1,475 m) to the confluence with the Shavers Fork (elevation = 1,174 m). As occurs in many Appalachian streams, brook trout are the only species present in headwater tributaries to the Second Fork. However, the Second Fork main stem supports additional species, including mottled sculpin *Cottus bairdii*, rosyside dace *Clinostomus funduloides*, longnose dace *Rhinichthys cataractae*, and eastern blacknose dace *R. atratulus*. Other trout species, such as brown trout *Salmo trutta* and rainbow trout *O. mykiss*, are rare in the Second Fork. The average stream width within the Second Fork varies from 2 m in the headwater tributaries to 10 m near the Shavers Fork confluence. Dominant substrates within the main stem of the Second Fork are composed of boulders, cobble, and occasional patches of gravel, whereas cobble and gravel substrates dominate the tributaries. As a

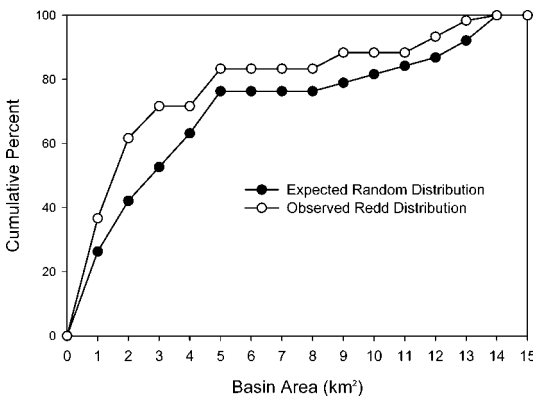


FIGURE 2.—Relationship between the observed cumulative frequency of brook trout redds and the expected pattern based on the accumulation of available stream segments along a continuum of basin area within the Second Fork watershed, West Virginia, in fall 2000.

result of variation in bedrock geology and other landscape features (e.g., beaver ponds), there is a high degree of variability in water quality and habitat characteristics among reaches within the Second Fork watershed. Consequently, the Second Fork provides an ideal setting for an examination of the combined effects of physicochemical features on brook trout population structure.

Methods

Water Temperature, Chemistry, and Instream Habitat

We deployed continuous temperature loggers (HOBO, Onset Computer Corp.) at each site to obtain measures of mean, maximum, and average July water temperatures ($\pm 0.1^\circ\text{C}$). Because of problems with high flows and ice, we obtained year-round data from three sites only. Consequently, we limited our temperature analysis to data collected from April 1 to November 1 in 2000 and 2001. Stream alkalinity (mg CaCO_3/L) and pH were determined from filtered water samples taken seasonally within each study site when the stream was at base flow (filter size = $0.45\ \mu\text{m}$; potentiometric titration to pH 4.5). Previous studies have identified alkalinity and pH as critical chemical parameters determining trout habitat quality in the Shavers Fork watershed (Clayton et al. 1998).

Habitat sampling was conducted in late spring of 2001 and followed a technique that combines visual estimation and transect-based sampling to quantify a variety of physical habitat parameters in each study site (Petty et al. 2003). Working in an upstream direction, we recorded habitat measurements at five evenly spaced locations along transects placed at intervals equal to one mean stream width. Measurements taken along transects included wetted channel width ($\pm 0.1\ \text{m}$), depth ($\pm 1\ \text{cm}$), average current velocity ($\pm 1\ \text{cm/s}$), bottom current velocity, dominant substrate type, distance to cover ($\pm 0.1\ \text{m}$), and cover type. Combined with the transect sampling, the following parameters were visually estimated: percent canopy cover, percent fish cover (instream and bank), percent of the wetted area as stream margin, percent of area suitable for brook trout spawning (based on flow, depth, and substrate composition), and the area of discrete hydraulic channel unit types. Hydraulic channel units were identified as homogeneous (e.g., riffle, glide, pool) or complex (e.g., riffle-run, riffle-glide) (Petty et al. 2003).

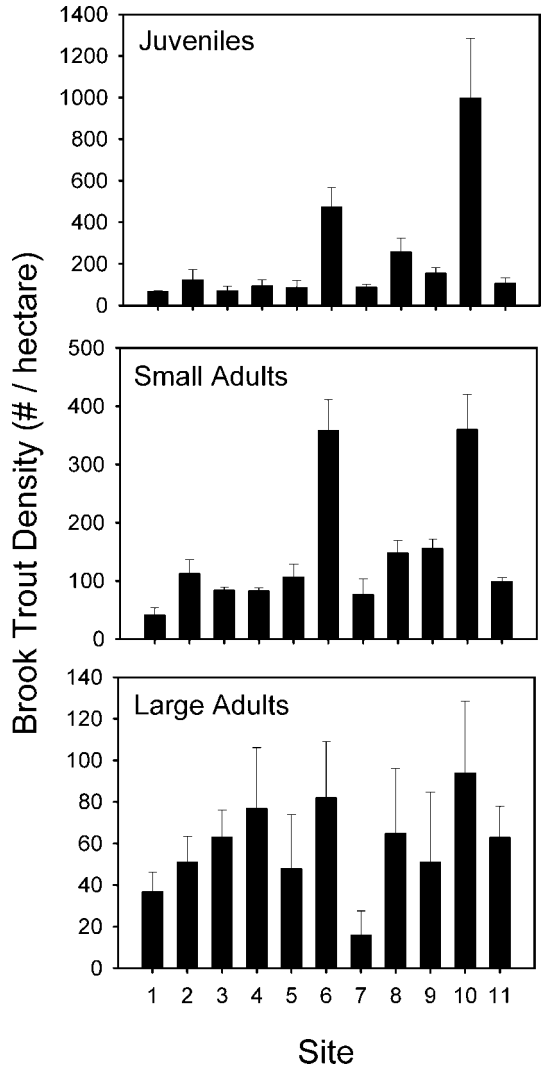


FIGURE 3.—Annual mean brook trout density (\pm SE) for three age-classes in 11 study reaches within the Second Fork watershed, West Virginia, sampled in 2000–2001.

Brook Trout Spawning

To quantify spatial variation in brook trout spawning intensity, we conducted redd count surveys (Beland 1996) continuously throughout the Second Fork watershed during the fall of 2000. The entire watershed, including the Second Fork main stem and its tributaries, was walked in both an upstream and downstream direction in an effort to locate brook trout engaged in spawning activity. Several different routes with different starting points were used for the survey to avoid spatial and temporal bias in identifying redd sites. The

TABLE 3.—Electrofishing capture probabilities (p) and brook trout abundance estimates (N), both \pm SE from three-pass depletion methods and application of the removal estimator for closed populations. Capture probabilities were equal among age-classes but not among seasons or sites. Abundance was estimated separately for juveniles, small adults, and large adults at each site for each season and was summed to produce a total population size for each site (presented here). The delta method (Peterson et al. 2004) was used to calculate the variance and SE associated with each total abundance estimate.

Season and parameter	Site					
	1	2	3	4	5	6
Spring 2000						
p	0.48 (0.06)	0.64 (0.06)	0.53 (0.06)	0.56 (0.07)	0.54 (0.08)	0.58 (0.05)
N	38 (2.0)	55 (2.4)	50 (2.3)	40 (2.1)	27 (1.7)	64 (2.6)
Summer 2000						
p	0.67 (0.09)	0.75 (0.07)	0.81 (0.06)	0.23 (0.16)	0.25 (0.16)	0.62 (0.09)
N	34 (1.1)	46 (0.9)	38 (0.0)	68 (7.6)	60 (6.6)	44 (1.6)
Fall 2000						
p	0.71 (0.09)	0.68 (0.07)	0.68 (0.07)	0.59 (0.07)	0.56 (0.09)	0.66 (0.07)
N	24 (0.0)	33 (1.0)	36 (21.0)	31 (2.0)	21 (1.6)	37 (1.3)
Spring 2001						
p	0.61 (0.11)	0.35 (0.10)	0.80 (0.05)	0.44 (0.11)	0.62 (0.14)	0.74 (0.06)
N	31 (1.4)	102 (6.2)	45 (0.0)	54 (3.4)	17 (1.0)	69 (1.1)
Annual mean						
p	0.62 (0.02)	0.60 (0.09)	0.71 (0.03)	0.45 (0.07)	0.49 (0.08)	0.65 (0.03)
N	32 (2.1)	59 (14.8)	42 (2.0)	48 (7.6)	31 (9.7)	53 (6.8)

survey routes were alternated between days, and surveys were conducted on 30 separate days between October 5 and November 24, 2000. We were unable to conduct surveys later in the year due to snowfall and increasing levels of ice cover. Subsequent observations in this watershed have indicated that brook trout spawning is essentially finished by early December, presumably because of low water temperatures (2–4°C).

When spawning activity was observed, the location was mapped by use of a Global Positioning System unit and topographical maps. For analytical purposes, we divided the watershed into a series of continuous, 300-m stream segments. Spawning intensity was quantified as the number of identified redds in a stream reach divided by the area of the reach (i.e., redd density). We unambiguously identified a redd site if (1) individuals were actively engaged in the deposition of eggs into the substrate or (2) individuals were holding in areas with evidence of recent egg deposition. We did not attempt to identify redds in the absence of spawning brook trout nearby. The size of redds constructed by brook trout in the Second Fork watershed were small (<0.1 m²), and consequently the visual evidence of redds quickly disappeared (P. J. Lamothe, personal observation). As a result, we adopted conservative criteria for redd identification (sensu Magee et al. 1996). We used ArcGIS software version 8.3 (Environmental Sys-

tems Research Institute 2003) to estimate the watershed area draining to each identified redd site. We also noted the channel unit type (e.g., pool, riffle, run, complex; sensu Petty et al. 2003) and dominant substrate type (e.g., silt, sand, gravel, cobble, boulder, bedrock) at the position of the redd site, and measured water depth, stream channel width, wetted width, stream pH, and water temperature.

Brook Trout Abundance, Survival, and Immigration

Eleven 100-m sampling sites were established in spring 2000 within the Second Fork watershed and were selected to cover a full range of physicochemical conditions (Table 1). Brook trout populations inhabiting these sites were sampled in spring 2000 (June 1–10), summer 2000 (August 1–10), fall 2000 (October 7–18), and spring 2001 (June 1–8). We used three-pass electrofishing procedures to capture brook trout and obtain estimates of brook trout abundance and population size structure at each study site during each season. Prior to sampling, the ends of each site were blocked with a fine-mesh seine (0.5 × 0.5 cm). Teams of three to five people (depending on stream size) captured brook trout with backpack electrofishing units (Smith-Root, DC, 60 Hz, 400–600 V) and a combination of dip nets and seine nets. All fishes captured were identified to species, anes-

TABLE 3.—Extended.

Season and parameter	Site				
	7	8	9	10	11
Spring 2000					
<i>p</i>	0.51 (0.07)	0.50 (0.06)	0.43 (0.07)	0.59 (0.07)	0.51 (0.08)
<i>N</i>	36 (2.0)	40 (2.1)	24 (1.6)	44 (2.2)	29 (1.8)
Summer 2000					
<i>p</i>	0.74 (0.07)	0.52 (0.13)	0.66 (0.11)	0.52 (0.08)	0.62 (0.10)
<i>N</i>	29 (0.0)	31 (2.0)	24 (1.0)	82 (3.2)	32 (1.4)
Fall 2000					
<i>p</i>	0.63 (0.11)	0.66 (0.08)	0.59 (0.09)	0.62 (0.05)	0.56 (0.07)
<i>N</i>	15 (0.0)	25 (0.9)	21 (1.3)	80 (3.3)	35 (2.7)
Spring 2001					
<i>p</i>	0.80 (0.10)	0.65 (0.08)	0.75 (0.09)	0.64 (0.05)	0.81 (0.09)
<i>N</i>	12 (0.0)	44 (1.4)	18 (0.0)	109 (2.3)	17 (0.0)
Annual mean					
<i>p</i>	0.67 (0.04)	0.58 (0.03)	0.61 (0.04)	0.59 (0.03)	0.63 (0.05)
<i>N</i>	23 (3.9)	35 (4.1)	22 (1.3)	78 (7.2)	28 (3.9)

thetized in clove oil (concentration = 40 mg/L), and measured for standard length (± 1 mm) and weight (± 0.1 g). At the time of first capture, brook trout were given a unique mark sequence (≥ 3 separate marks each) with colored elastomer dyes (Northwest Marine Technology). The dye was injected between the rays of the caudal and/or anal fins. Use of four colors and multiple fin locations allowed for unique individual marks. Our marking approach also reduced the likelihood of complete mark loss, because a fish would have to lose marks from at least three locations to be incorrectly identified as an unmarked individual. After marking, we returned all fish to their approximate location of capture.

For each seasonal sample, we separated brook trout into three age-classes based on length-frequency distributions of data pooled from the 11 study sites (Figure 1). The juvenile class is a true representation of age and represents individuals known to have been produced the previous fall. The small-adult and large-adult class distinctions were based on length-frequency histograms but probably do not represent a true distinction in age.

Statistical Analyses and Hypothesis Testing

Brook trout spawning and the distribution of juveniles and adults.—Our first objective was to quantify the physical and chemical characteristics of areas within the Second Fork watershed that are

used for spawning by brook trout. We used stepwise multiple regression to determine which physical and chemical variables were most important in predicting brook trout spawning intensity. Variables previously shown to be important to brook trout spawning site selection (Witzel and MacCrimmon 1983) and juvenile habitat suitability (McLaughlin et al. 1994) were selected for the analysis and included stream width, basin area, availability of cover, stream pH, and alkalinity. All variables were log-transformed to ensure normality. Variables were included in the regression model if the *P*-value was less than 0.15. The significance level (α) used for acceptance of the overall model was 0.05. All statistical tests were judged at this significance level unless otherwise noted. We also were interested in determining specific stream sizes that were most important to brook trout spawning. Kolmogorov–Smirnov tests were used to compare the observed cumulative frequency of brook trout redds with the expected cumulative frequency of stream segments available for spawning along a continuum of basin area. Basin area data for this analysis were from the 300-m-segment scale, and the basin area for a given segment was assigned to all redds within the segment. The analysis tested the hypothesis that brook trout disproportionately focus spawning activities within streams of a particular size.

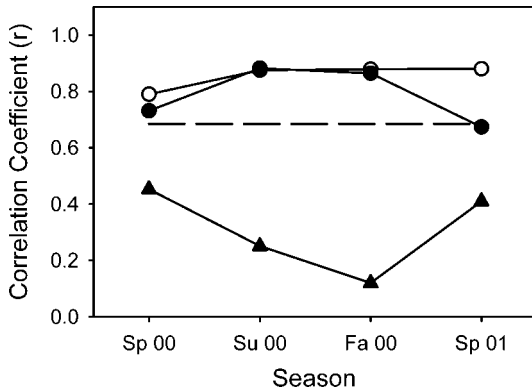


FIGURE 4.—Correlations between brook trout spawning intensity in fall 2000 and the densities of juveniles (open circles), small adults (filled circles), and large adults (filled triangles), in each seasonal sample from the Second Fork watershed, West Virginia. Points above the dashed line represent significant positive correlations ($\alpha = 0.05$). Bonferroni's criterion was used to adjust α to account for multiple statistical tests on the same data set (significance at $P < 0.0127$).

Our second objective was to determine the extent to which spatial variation in brook trout spawning intensity was correlated with the distribution of juvenile and adult brook trout within the Second Fork watershed. Simple correlation analysis was used to relate redd density to densities of the three brook trout age-classes (i.e., juvenile, small adult, and large adult), and the Bonferroni method (Zar 1999) was used to control experimentwise error rates associated with multiple non-orthogonal tests ($\alpha = 0.0127$). An associated objective was to identify additional environmental factors that might influence the distribution of brook trout in the Second Fork watershed. We used stepwise multiple regression to produce models for predicting the seasonal abundance of brook trout in different areas of the watershed. Variables used to construct each seasonal model were taken from our habitat and water quality surveys. However, to avoid redundancy with previous analyses, we did not include variables that were important predictors of brook trout spawning intensity.

A secondary objective was to quantify the degree of temporal stability in brook trout distributions within the Second Fork watershed. We used correlation analysis to assess changes in the relative abundance of each age-class among the 11 sample reaches. High stability in the distribution of a given age-class would result in a high correlation in brook trout density between subsequent seasons and years. This analysis was conducted

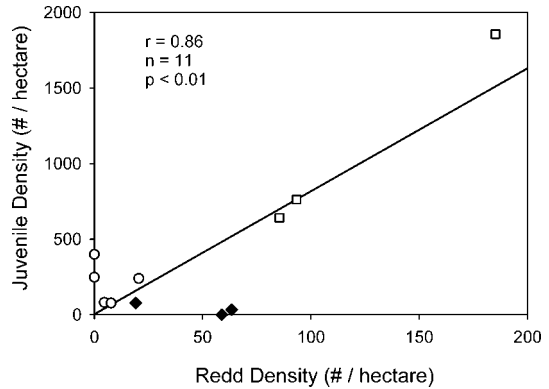


FIGURE 5.—Linear relationship (statistics given are from correlation analysis) between brook trout spawning intensity at a given site (fall 2000) and juvenile density at that same site during the following year (spring 2001). Symbols represent sites with the following alkalinity levels: <7 mg CaCO₃/L (filled diamonds), 7–15 mg CaCO₃/L (open circles), and >15 mg CaCO₃/L (open squares).

separately for the following seasonal pairs: spring–summer 2000, summer–fall 2000, fall 2000–spring 2001, and spring 2000–spring 2001.

Apparent survival and immigration.—Our final objective was to quantify the effects of age, spatial position, and season on brook trout survival and immigration rates. We used mark–recapture data and maximum likelihood estimators in the program MARK to quantify demographic rates separately for each age-class at each site in each season (White and Burnham 1999). Our analyses to estimate brook trout population parameters (electrofishing capture probability, abundance, apparent survival, and immigration) followed Pollock's robust design (Peterson et al. 2004). We assumed that populations within each site were (1) closed to gains (from births and immigration) and losses (from deaths and emigration) during each seasonal sample and (2) open between subsequent seasonal samples.

Data from three-pass depletion sampling and the generalized removal estimator for closed captures (White et al. 1982) were used to estimate brook trout abundance and capture probability for each site, season, and age-class. This information was then used in open population estimators to quantify season-, site-, and age-class-specific survival and immigration. We used the Cormack–Jolly–Seber model in MARK to estimate apparent survival ($1 - [\text{mortality} + \text{emigration}]$) and the Pradel model (recruitment only) to estimate brook trout immigration. Akaike's information criterion correct-

TABLE 4.—Summary results of multiple linear regression analyses relating large-adult brook trout density (dependent variable) to various stream habitat variables (excluding basin area and alkalinity) in the Second Fork watershed, West Virginia. None of the measured variables explained a significant ($P < 0.05$) amount of variation in large-adult density in spring 2000 or spring 2001 or in small-adult or juvenile density in any season.

Season	Habitat variable	<i>F</i>	df	R^2	Direction of effect	<i>P</i>
Summer 2000	% Canopy cover	37.5	10	0.65	–	0.003
	Wetted stream width	8.2	10	0.18	+	0.02
	Average water depth	4.7	10	0.07	+	0.07
	Full model	20.5	10	0.90		0.008
Fall 2000	% Stream margin	4.4	10	0.33	–	0.07
	% Spawning substrate	4.2	10	0.23	+	0.07
	Full model	5.1	10	0.56		0.04

ed for small-sample bias (AIC_c) was used to assess the interactive effects of season and site variation on capture probability and brook trout survival and immigration (Burnham and Anderson 2002) (Table 2).

Because individuals were able to move into and out of each study site between seasonal samples, we modeled apparent survival such that a fish that emigrated from a study reach was essentially the same as a fish that died. Occasionally (28 of 1,621 captures), an emigrant from one reach was recaptured in another reach. However, because these events were relatively rare, the information could not be used to obtain a reliable estimate of site-, season-, or age-class-specific emigration rates. Consequently, capture histories for those individuals were modified to reflect loss from one reach and addition to another. Nevertheless, this infor-

mation could be used to obtain site-, season-, and age-class-specific estimates of immigration (i.e., in Pradel model applications). Because juvenile brook trout were too small to be effectively marked in spring 2000, capture history data were analyzed separately for each age-class.

We used one-way analysis of variance to test for seasonal variation in brook trout demographic rates for each age-class separately. In addition, we examined spatial trends in brook trout survival and immigration. Specifically, linear and nonlinear regression methods were used to relate spatial variation in age- and site-specific demographic rates to basin area.

Results

Brook Trout Spawning Intensity

We identified 60 distinct brook trout redds in the Second Fork watershed during fall 2000. Microhabitat measurements taken at the time of spawning indicate that brook trout spawned most frequently in the tail sections of pools (34 of 60 observations) or in the heads of low-gradient riffles (12 of 60 observations). Spawning occurred in locations with an average depth of 41 cm (range = 20–70 cm) and with substrate comprised primarily of gravel. Stream pH in spawning locations ranged from 5.4 to 7.3 (mean = 6.4).

Stepwise multiple regression produced a highly significant model relating environmental variables to brook trout spawning intensity (full model: $F = 24.96$, $df = 10$, $P < 0.001$, $R^2 = 0.91$). Variables that best predicted brook trout spawning site selection within the watershed included basin area ($P < 0.01$, $R^2 = 0.73$), stream alkalinity ($P = 0.05$, $R^2 = 0.11$), and the amount of available cover ($P = 0.05$, $R^2 = 0.07$). The importance of basin area to redd site selection by brook trout was illustrated further by comparing the cumulative frequency of redd sites in different-size streams with the cu-

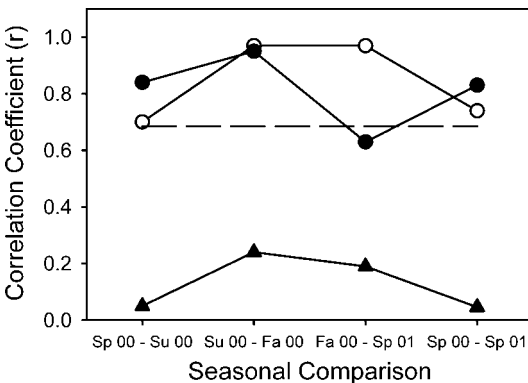


FIGURE 6.—Interseasonal correlations in brook trout density for juvenile (open circles), small-adult (filled circles), and large-adult (filled triangles) brook trout at 11 sample sites in the Second Fork watershed, West Virginia, 2000–2001. Points above the dashed line represent significant positive correlations ($\alpha = 0.05$). Bonferroni’s criterion was used to adjust α to account for multiple statistical tests on the same data set (significance at $P < 0.0127$).

TABLE 5.—Mean \pm SE apparent survival (ϕ) and immigration (Γ) rates of juvenile, small-adult, and large-adult brook trout, averaged across 11 segments of the Second Fork watershed, West Virginia. Juvenile ϕ and Γ could not be estimated (CNE) in the spring–summer (SP–SU) 2000 interval because juveniles were too small to mark in the spring. Juvenile Γ estimates for the fall (FA) 2000–spring 2001 interval are not applicable (NA) because juveniles in fall 2000 were small adults in spring 2001. Letters indicate significant differences ($P < 0.05$) in ϕ or Γ among seasonal intervals within each age-class.

Parameter and age-class	Seasonal interval			Annual mean
	SP–SU 2000	SU–FA 2000	FA2000–SP2001	
Apparent survival (ϕ)				
Juveniles	CNE	0.293 (0.046) ^a	0.139 (0.024) ^b	0.218 (0.149)
Small adults	0.597 (0.049) ^z	0.463 (0.037) ^{zy}	0.317 (0.046) ^y	0.459 (0.081)
Large adults	0.432 (0.039)	0.405 (0.087)	0.309 (0.111)	0.382 (0.037)
Immigration (Γ)				
Juveniles	CNE	0.630 (0.138)	NA	0.630 (0.138)
Small adults	0.561 (0.106)	0.236 (0.057)	0.561 (0.211)	0.452 (0.108)
Large adults	0.350 (0.139) ^y	0.110 (0.057) ^y	0.852 (0.394) ^z	0.437 (0.219)

mulative availability of stream reaches in the watershed (Figure 2). A Kolmogorov–Smirnov test of these curves indicated that brook trout tended to spawn in streams draining small basin areas at a rate that was disproportionate to their availability in the watershed (D_{\max} [the maximum distance between the observed and expected curves] = 0.26, $n = 60$, $P < 0.001$). In fact, nearly 80% of spawning by brook trout occurred in stream segments draining basin areas of 3.0 km² or less (Figure 2).

Juvenile and Adult Brook Trout Distribution and Abundance

We captured 1,621 brook trout within the 11 study sites during the four seasons of the study. The distribution of brook trout among the sites was highly variable, and patterns differed depending on the age-class examined (Figure 3; Table 3). Correlation analysis indicated a significant positive relationship between local spawning intensity in fall 2000 and the density of juvenile and small-adult brook trout in each seasonal sample (Figure 4). In contrast, we did not observe a significant relationship between spawning intensity and large-adult density in any season (Figure 4), suggesting that the seasonal distribution of larger brook trout may be influenced by factors unrelated to the reproductive process.

An examination of the relationship between spawning intensity in fall 2000 and juvenile density in spring 2001 illustrates the combined importance of spawning intensity and alkalinity in determining brook trout recruitment (Figure 5). Figure 5 shows that the relationship between spawning intensity and juvenile density is strongly influenced by stream alkalinity. Specifically,

streams with alkalinities less than 7 mg CaCO₃/L experienced negligible levels of juvenile recruitment, regardless of the level of spawning activity observed during the previous fall (Figure 5).

Multiple-regression analysis indicated that environmental variables were much stronger determinants of large-adult distribution than spawning intensity was. The specific variables that could be used to predict large-adult brook trout distribution, however, varied seasonally (Table 4). We found no significant variables to explain large-adult brook trout distribution in spring 2000 and 2001. However, large-adult density in summer 2000 was highest in stream reaches with open canopies, greater widths, and relatively deep microhabitats (Table 4). In contrast, large-adult density in fall 2000 was highest in areas with higher amounts of suitable spawning habitat and lower amounts of stream margin. Similar analyses conducted on juveniles and small adults to explain their distributions failed to identify any significant variables that were not associated with spawning intensity (e.g., basin area, alkalinity).

Juvenile and small-adult brook trout distributions within the Second Fork watershed were temporally stable over the course of our study. We found a significant degree of seasonal and year-to-year correlation in within-site densities of juvenile and small-adult brook trout (Figure 6). In other words, sites with high densities of juveniles and/or small adults tended to remain high density over successive seasons, whereas low-density sites tended to remain so. In contrast, large-adult brook trout distribution was unstable, and we observed significant seasonal and year-to-year shifts in density. These shifts resulted in a low correlation be-

tween within-site densities of large-adult brook trout for successive seasons (Figure 6).

Brook Trout Survival and Immigration

We observed significant seasonal variation in the demographic rates experienced by different brook trout age-classes (Table 5). Across seasons, juveniles experienced lower apparent survival and higher immigration rates than did small and large adults (Table 5). Small-adult brook trout exhibited high, relatively stable survivorship; an average of nearly 50% of individuals remained within a given study site over seasonal intervals (Table 5). In contrast, large adults experienced slightly lower apparent survival rates than small adults did, and the immigration rates of large adults were highly variable (11–85%; Table 5).

We also observed significant spatial variability in demographic rates exhibited by different age-classes (Figures 7, 8). All three age-classes experienced higher apparent survival rates in the smallest streams during the summer–fall 2000 interval (Figure 7). A similar pattern was observed for large adults during the fall 2000–spring 2001 interval: large-adult survival within a given site was low except in the two smallest headwater streams (Figure 7). Interestingly, the immigration rate of large adults followed the opposite pattern; the greatest rates occurred in larger stream segments in the summer–fall and fall–spring intervals (Figure 8). We observed no consistent relationship between basin area and immigration rates of juveniles and small adults in any season, although there was considerable site-to-site variability in immigration rates of these age-classes (Figure 8).

Summed estimates of apparent survival and immigration provided a measure of site- and season-specific population growth rate for each brook trout age-class and demonstrated the extent to which changes in population size were influenced by dispersal and local survivorship (Figure 9). Although juvenile survival was highest in the smallest streams, apparent survival was low relative to immigration. Consequently, the rate of juvenile population change within a site primarily was governed by site-dependent differences in juvenile immigration (Figure 9). The relative contributions of survivorship and immigration to the population growth of small adults, however, were more balanced during the spring–summer and summer–fall 2000 intervals. Nevertheless, for the fall 2000–spring 2001 interval, dramatic spatial variability in small-adult immigration rate was the dominant mechanism influencing small-adult distribution

throughout the Second Fork watershed (Figure 9). Finally, the relative contributions of survivorship and immigration to large-adult population growth rate were highly variable from season to season. In the spring–summer 2000 interval, there was considerable spatial variability in large-adult immigration, which largely determined site-to-site variation in population growth rate (Figure 9). Extremely low rates of large-adult immigration in the summer–fall 2000 interval, however, resulted in declining populations throughout the watershed. In contrast, high rates of large-adult immigration produced dramatic increases in population growth rate for the larger stream segments during fall 2000–spring 2001, whereas large-adult populations in smaller headwater sites were not influenced by immigration (Figure 9). Presumably, new adult immigrants to larger sites in the Second Fork during spring 2001 came from the Shavers Fork main stem.

Discussion

Brook Trout Spawning

Stream size was the most important factor influencing where brook trout focused their spawning efforts in the Second Fork watershed. Nearly 80% of all spawning observed in the watershed occurred in tributaries with a basin area less than 3 km². To a lesser extent, stream alkalinity and the amount of instream cover also influenced brook trout spawning in the watershed. Surprisingly, there are very few extant published studies on spawning by stream-resident brook trout against which to compare our results (Witzel and MacCrimmon 1983; Curry and Noakes 1995; Essington et al. 1998), and only one of those was conducted in the Appalachian region (Curry and Noakes 1995). Generally, these studies have demonstrated the importance of groundwater upwelling to redd site selection by brook trout. Witzel and MacCrimmon (1983) found that brook trout inhabiting southwestern Ontario streams focused reproductive efforts in headwater areas, where groundwater inflows maintained stable temperature, flow, and chemical conditions. Essington et al. (1998) found that brook trout in a Minnesota watershed preferred spawning sites in relatively deep areas with upwelling groundwater. Access to groundwater probably is an important determinant of brook trout spawning in Appalachian watersheds and may explain why small tributaries were so important to brook trout reproduction in the Second Fork. Nevertheless, additional studies are

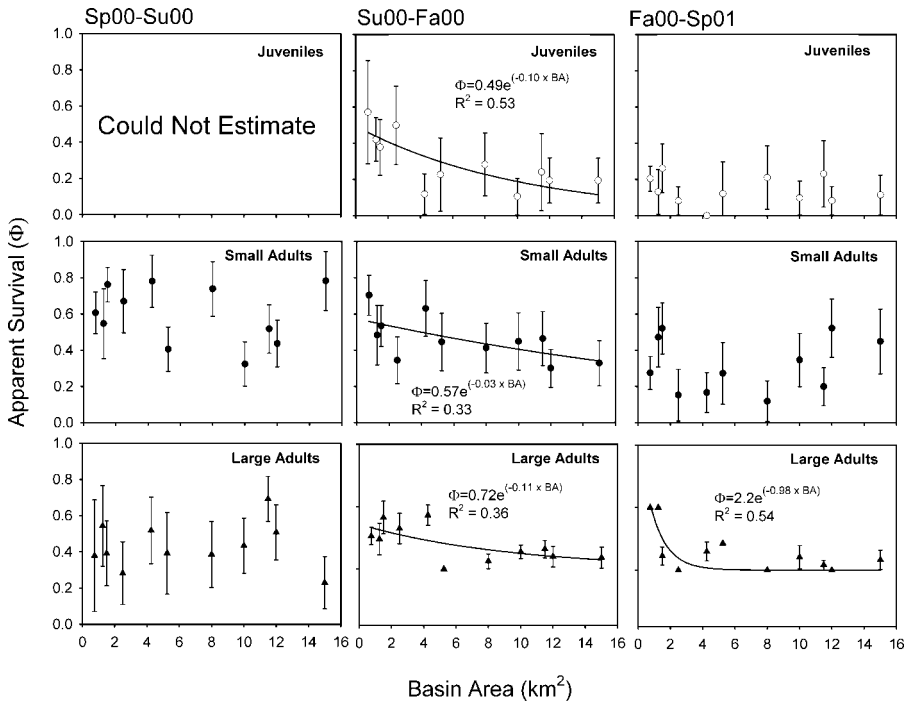


FIGURE 7.—Relationships between apparent survival (Φ) and basin area for juvenile, small-adult, and large-adult brook trout in the Second Fork watershed, West Virginia, 2000–2001. Vertical bars represent 95% confidence intervals. Fitted regression lines were significant at $P < 0.05$. Juvenile Φ could not be estimated for the spring–summer 2000 interval because juveniles could not be marked in spring. Abbreviations are as follows: Sp = spring, Su = summer, and Fa = fall.

needed to confirm the importance of groundwater to brook trout reproduction in the central Appalachian region.

An additional explanation for the importance of small streams to brook trout spawning is that high, bed-moving flows are rare during egg incubation periods (i.e., October–March) in small Appalachian streams (Sun et al. 2002). Although high flows in winter and early spring are common in larger streams, small Appalachian streams often experience their highest flows during summer thunderstorms and tropical storms (Roghair et al. 2002; Carline and McCullough 2003). The effect of streambed-altering flows on the spatial distribution of brook trout in Appalachian watersheds warrants additional research, especially considering the effects of floods on the temporal dynamics of trout populations (Spina 2001; Cattaneo et al. 2002).

Finally, small headwater streams also may be preferred spawning areas for brook trout because they protect larvae and juveniles from predators and potential competitors. Many of the key reproductive areas in the Second Fork watershed are too

shallow to support large brook trout year-round. In addition, these areas tend to be devoid of other species (e.g., sculpins) that may be effective competitors with or predators of small brook trout.

Reproductive Success and Juvenile Recruitment

Spatial variation in brook trout spawning was an important determinant of the distribution of juvenile brook trout within the Second Fork watershed. This conclusion is supported by two findings. First, we observed a significant relationship between spawning intensity in fall 2000 and juvenile density during the following spring. Second, we observed strong seasonal stability in juvenile brook trout distribution at the watershed scale, which means that the relative abundance of this age-class within different areas of the watershed remained constant from season to season.

These findings are consistent with numerous other studies of stream-dwelling salmonids. (Beard and Carline 1991; Bozek and Rahel 1991; Beland 1996; Magee et al. 1996; Knapp et al. 1998). Beard and Carline (1991) observed a positive linear relationship between reproductive ef-

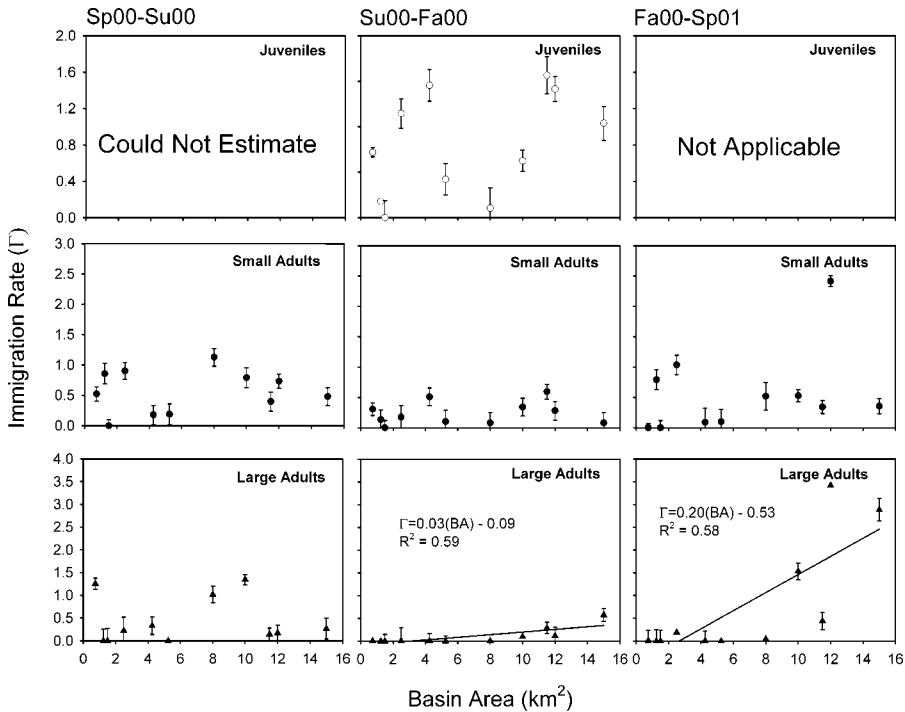


FIGURE 8.—Relationship between immigration rate (Γ) and basin area for juvenile, small-adult, and large-adult brook trout in the Second Fork watershed, West Virginia, 2000–2001. Vertical bars represent 95% confidence intervals. Fitted regression lines were significant at $P < 0.05$. Juvenile Γ could not be estimated for spring–summer 2000 and was not applicable for fall 2000–spring 2001. Abbreviations defined in Figure 7.

fort by brown trout and juvenile density during the following year in Appalachian streams. Knapp et al. (1998) observed a similar relationship for California golden trout *O. mykiss aguabonita*. These investigators went on to argue that such a relationship provides evidence that spawning habitat is a critical factor limiting many stream-dwelling trout populations (Knapp et al. 1998). Because our study was not designed to address this question directly, we hesitate to draw a similar conclusion. However, our results support the hypothesis that brook trout populations in the Second Fork may be limited by reproductive success.

Seasonal stability in the distribution of juveniles suggests that individuals within this age-class do not disperse long distances from where they were spawned. A thorough review of the mark–recapture results, however, indicates that this conclusion may not be correct. Juvenile immigration rates were relatively high throughout the watershed during the summer–fall 2000 interval; the mean immigration rate was 0.63. High rates of immigration coupled with low survival rates overall resulted in a high turnover rate of juveniles within any given reach,

which suggests a relatively high rate of juvenile mobility (Gowan et al. 1994; Rodriguez 2002). Despite the high rate of turnover, juvenile distributions were stable over time because juvenile survival was highest within small tributaries. Consequently, spatial variation in juvenile survival tended to amplify the spatial pattern initially set by spawning and juvenile recruitment.

Despite the positive effect of spawning intensity on juvenile recruitment, ultimate reproductive success was influenced by water chemistry. This conclusion is based on an examination of the relationship between juvenile density in spring 2001 (i.e., reproductive success), spawning intensity in fall 2000 (i.e., reproductive effort), and alkalinity. Although reproductive success depended on reproductive effort and therefore stream size, successful reproduction was observed only in streams where alkalinity exceeded 7 mg CaCO_3/L . Reduced survival of brook trout eggs and larvae in streams with low alkalinity and pH has been well documented (Menendez 1976; Kwain and Rose 1985; Baker et al. 1996; Van Sickle et al. 1996). Numerous physiological mechanisms can cause

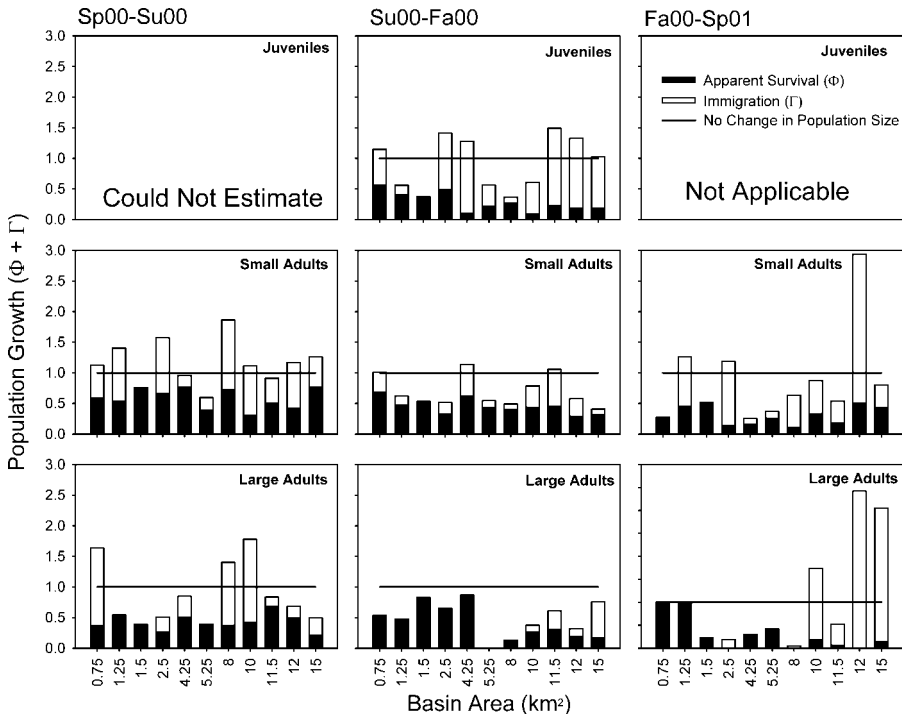


FIGURE 9.—Spatial and seasonal variation in population growth rates of juvenile, small-adult, and large-adult brook trout in the Second Fork watershed, West Virginia, 2000–2001. Estimates are presented for each of 11 study sites sorted by basin area. The horizontal line represents a population growth rate of 1.0, where immigration (Γ) and survival (Φ) combine to produce a stable population. Abbreviations defined in Figure 7.

mortality in acidified streams, but the critical factor in Appalachian streams appears to be elevated concentrations of dissolved monomeric aluminum during acidic episodes (Mount et al. 1988). Another important factor appears to be the timing and duration of acidic episodes (DeWalle et al. 1995). Acidic episodes that occur during periods of larval emergence from redds can cause extremely high rates of mortality (Jordahl and Benson 1987; Fiss and Carline 1993). Furthermore, long-duration acidic episodes (i.e., >24 h) can cause egg, larval, and juvenile brook trout mortality rates that are significantly higher than those produced by brief events (Van Sickle et al. 1996).

Our observation that brook trout attempted unsuccessfully to reproduce in several small, low-alkalinity streams suggests that these areas may act as “attractive sinks” (Delibes et al. 2001). Most streams in this region of the Appalachian Mountains are not chronically acidic but are prone to severe acidic episodes (Wigington et al. 1996). During low-flow periods, stream pH often exceeds 6.0, even in areas with zero alkalinity (Lamothe 2002). However, during acidic episodes, pH levels

in low-alkalinity streams may drop from 6.5 to below 4.0 (Wigington et al. 1996). Johnson and Webster (1977) found that brook trout would avoid areas with pH levels below 5.0; however, above this level, brook trout did not discriminate based on pH. Consequently, during extended low-flow periods, small, low-alkalinity streams may attract spawning adult brook trout from other areas in a watershed. They are attractive as reproductive habitats because they possess relatively high pH levels and low densities of other adults that may potentially compete for spawning sites and food. However, spring rains and snowmelt ultimately overwhelm the buffering capacity of these streams, resulting in complete or partial reproductive failure (Lamothe 2002). The possibility that small, acidic streams may act as reproductive traps within Appalachian watersheds has important implications for trout stream remediation programs. For example, management plans that include limestone fine additions (Clayton et al. 1998) may need to consider where those additions are placed and how acidic stream segments in the watershed may affect trout population recovery in treated areas.

Spatial Dynamics of Adult Brook Trout

The distribution of small-adult brook trout within the Second Fork watershed appears to be influenced by the same processes that affect reproductive success and juvenile recruitment. Again, two findings support this conclusion: (1) a positive linear relationship between juvenile and small-adult densities, and (2) strong season-to-season stability in the distribution of small adults. As with juveniles, these findings support the hypothesis that recruitment processes may limit the abundance of small adults within the Second Fork watershed (Knapp et al. 1998). In contrast to juveniles, however, small adults exhibited relatively high survival rates and lower rates of immigration. Consequently, within-site turnover rates of small-adult brook trout were relatively low, perhaps indicating low rates of mobility by this age-class.

Large-adult distribution, in contrast, was strongly influenced by postreproductive processes, and factors other than those influencing reproduction may determine the abundance and distribution of large adults in the Second Fork watershed. Large-adult density was not correlated with spawning intensity, and large-adult distribution was highly unstable from season to season. This finding is inconsistent with that of Beard and Carline (1991), who found significant positive relationships between spawning effort and all size-classes of brown trout in Appalachian streams. In contrast, our results suggest that the spatial and temporal variation in apparent survival combines with that of immigration to determine large-adult distribution at the watershed scale. Mark-recapture data indicate that large-adult populations exhibit considerable spatial and seasonal variation in apparent survival and immigration, thereby producing a high rate of population turnover within any given stream segment.

These findings indicate that large adults may be significantly more mobile than small adults and may potentially use that mobility to access seasonally important habitats distributed throughout the watershed. For example, we found that large adults inhabited larger-sized stream reaches with reduced canopy cover in summer months. Additional research in this watershed has found that these areas possess benthic invertebrate density and biomass that are orders of magnitude higher than those of small, low-light reaches (Bopp 2002). In fall, however, large-adult density tends to be highest in areas possessing large amounts of suitable spawning substrates. Because ideal

spawning areas often do not overlap spatially with ideal foraging areas, higher rates of mobility may allow large adults to access seasonally important resources that are distributed at a watershed scale. To our knowledge, our study is the first to examine these questions as they relate to wild brook trout populations in the central Appalachian Mountains, and consequently, such questions should be a focus of future research in this region.

Management Implications

Protection and recovery of small tributaries (i.e., those draining basin areas less than 3 km²) are absolutely essential to the recovery of brook trout populations in the upper Shavers Fork watershed and perhaps throughout the central Appalachian Mountains. These streams are critical areas for brook trout spawning and juvenile recruitment. Identification and protection of ideal brook trout spawning habitat should be management priorities in the central Appalachian region. Once these areas are identified, artificial barriers like improperly installed culverts should be removed or redesigned to allow fish passage. Furthermore, acid remediation programs (e.g., Clayton et al. 1998) should attempt to recover streams located as high in the watershed as possible through use of existing roads and railroads or through aerial application of limestone.

Spawning, juvenile recruitment, differential survival, and dispersal interact to determine brook trout population dynamics at the watershed scale. Consequently, effective management of Appalachian brook trout fisheries will require a watershed-scale approach. This is especially true for populations with a large, highly mobile fraction, such as the population inhabiting the upper Shavers Fork watershed. Small tributaries are important for reproduction and as refuge and feeding habitats for young trout. Small, alkaline tributaries can be viewed as nonsubstitutable, complementary habitats (Schlosser and Angermeier 1995) required for population persistence within the watershed. However, larger trout require access to high-quality foraging habitats distributed at a watershed scale. Large, open-canopy, productive stream reaches can be viewed as substitutable, supplementary habitats (Schlosser and Angermeier 1995) required to maximize population productivity at the watershed scale. Watershed-scale management approaches are needed to improve linkages between the large water bodies used as supplementary feeding habitats and the small, alkaline streams that are the source of juvenile brook trout recruitment. Only then will it

be possible to ensure persistence and maximize recovery rates and productivity of Appalachian brook trout populations.

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