Movement, Growth, and Production of Brown Trout in Sympatry with Brook Trout in a Southern Appalachian Stream

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Abstract: A 1,532-m reach of Laurel Fork, a second-order tributary of the Doe River, Tennessee, was divided into 37 study sections which were sampled every 3 months by electrofishing. Brown trout *(Salmo trutta)* and brook trout *(Salvelinus fontinalis)* were weighed, measured, given a unique mark, and returned to the section from which they were caught. Population estimates were made with the Jolly Seber technique. Movement, density, instantaneous growth rate, biomass, and production were calculated. A large portion of recaptured brown trout (87%) and brook trout (63%) had trimonthly movements <75 m. Small sample sizes precluded calculating growth and production for brook trout. Mean instantaneous growth rates for brown trout were highest in August–October (0.45 and 0.77) followed by February–April (0.41), May–July (0.18), and November–January (0.13). Like growth rate, production was highest in the early fall (3.44 kg/ha) followed by early spring (2.48 kg/ha), early summer (2.29 kg/ha), and early winter (0.81 kg/ha). Total annual brown trout production in Laurel Fork was 9.02 kg/ha. The majority of this production (4.16 kg/ha or 46%) was by age 1 fish, though this was not significantly different from age 2 production (3.33 kg/ha or 37%). Older fish, ages 3 and 4 combined (1.06 kg/ha or 12%) were not significantly different from age 0 (0.47 kg/ha or 5%). The annual production to biomass ratio (P/B) for brown trout (0.85) was calculated using the mean biomass (10.6 kg/ha) and total annual production (9.02 kg/ha).

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The southern Appalachian highlands represent the southernmost extent of natural trout water in the eastern United States. Brook trout is the native salmonid in this area, while rainbow trout *(Oncorhynchus mykiss)* and brown trout were introduced early in this century and have become widely naturalized. Southern Appalachian brook and rainbow trout have been studied in depth (e.g., King 1937, Whitworth and Strange 1983, Larson and Moore 1985, Konopacky and Estes 1986, Nagel and Deaton 1989, Larson et al. 1995, Strange and Habera 1998). Little has been published on brown trout despite the fact that they are widely distributed and are the dominant salmonid in some streams. The objective of our study was to determine movement, growth, and production of brown trout in a stream where they were sympatric with brook trout.

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Methods

Study Area

The study was conducted on a 1.532-m reach (963 to 982 m elevation) of Laurel Fork, a second-order tributary of the Doe River in Carter County, Tennessee. The entire reach is within the Cherokee National Forest. The upper site boundary was an old beaver dam that was a substantial, but not impenetrable, barrier to trout movement. No barrier to trout movement was present below the study site for approximately 2 km. Three small first-order tributaries entered Laurel Fork within the study area. Historically, Laurel Fork was stocked with rainbow, brown, and brook trout. Currently, stocking is limited to catchable-sized rainbow trout outside the Forest Service boundary about 10 km downstream of the study section. The main stem of Laurel Fork is dominated by naturalized brown trout and the tributaries by brook trout (hybrids of northern and southern strains) (Kriegler et al. 1995, Saidak 1995). Angling was assumed to be minimal (none was detected during the study) and the majority of trout captured in the study section would have been under the minimum size limits (brown trout, 230 mm; brook trout, 150 mm).

The study reach was low gradient (12 m/km or 1.2%) with a mean width of 5.36 m and a mean depth of 0.22 m. Most pools averaged just over 0.5 m in depth but did not exceed 1 m in any part of the study area. The pool-riffle ratio was calculated to be 0.73:1 and the substrate was primarily cobble (26%), bedrock (23%), gravel (19.5%), boulder (16%), and sand (13.5%). Silt and organic material made up the remaining 2%. Riparian vegetation was predominantly rhododendron, hemlock, birch, maple, and mountain laurel. During our study, water temperatures ranged from 2.5 to 19.5 C and discharge from 0.07 to 0.40 m^3/second. Conductivity averaged 35.4 μ S/cm, alkalinity 16.3 mg/liter, and pH ranged from 6.8 –7.0.

Data Collection

The study area was divided into 37 contiguous sections, which ranged from 19 to 66 m and averaged 41 m in length. Sections were terminated at natural breaks in the stream channel such as small falls or cascades. Fish were sampled every 3 months to minimize the bias on behavior and growth rates caused by repeated electroshocking

(Gatz et al. 1986). Sampling was conducted 6 times: July and October 1996, and January, April, July, and October 1997. This resulted in 6 3-month intervals of early fall 1996 (Aug, Sep, Oct), early winter (Nov, Dec, Jan), early spring (Feb, Mar, Apr), early summer (May, June, July) and early fall 1997 (Aug, Sep, Oct). A single pass with 2 backpack electrofishing units (400 V AC, 1A) was used for each sampling following the procedure recommended by Habera et al. (1992). Block nets were not used between sections; natural barriers at the upstream ends of the sections minimized trout movement during shocking. After collection, fish were anesthetized (tricaine methanesulfonate), weighed, measured for total length, and checked for marks. Unmarked fish were given a unique code with either a visible implant tag (VIT) in the clear postocular tissue for fish over 130 mm or a cold brand (liquid nitrogen) for smaller fish (Raleigh et al. 1973). All fish received an adipose clip as a second mark. Scales were taken for age determination. After recovery from anesthesia, fish were returned to the section from which they were collected. Because the fish in Laurel Fork were relatively small (<250 mm in length), injury and mortality caused by electrofishing was expected to be minimal (Habera et al. 1996).

Data Analysis

In order to determine production, population estimates were calculated with JOLLY, a computer software package described by Pollock et al. (1990) based on the Jolly-Seber estimation technique (Jolly 1965). The open model (allowing both mortality/emigration and recruitment/immigration) was used requiring that a complete capture history be known for each fish in the population. In cases of tag loss, fish were randomly redistributed among previously captured fish of the same age that were not captured after the particular tag loss occurred. For each sample date, one population estimate was generated for all sections combined. JOLLY also calculated survival rates between intervals.

Instantaneous growth rates and production estimates were calculated for brown trout using the formulas in Bagenal (1978) and Ricker (1958). Brook trout sample sizes were too small to calculate growth and production. Instantaneous growth rates were estimated only for brown trout captured in successive samples. Instantaneous growth rate and production estimates were calculated separately for each age group. Where sample size was insufficient to estimate growth rate, the growth rate for an adjacent age class was used (this accounted for <10% of the total estimated production). Instantaneous growth rate for brown trout calculated for each 3-month interval was multiplied by the biomass estimate at the beginning of the interval to get the production estimate (kg/ha). Density and biomass, and thus production, could not be calculated for the first sample period because the Jolly-Seber model required at least one sampling period before and after each estimate. Variances were estimated following the methods of Neuman and Martin (1983). Means were considered significantly different if 95% confidence limits (2 standard errors) failed to overlap. Age class was determined by counting scale annuli. We have verified out scale aging with brown trout otoliths from Laurel Fork and other Tennessee streams and they agree very well up to age 4 (Habera et al. 2000). Mean trimonthly movement was calculated for all recaptures by dividing the distance moved by the number of intervals between captures.

Results

Movement

There were 315 recaptures with readable marks (82% brown trout, 18% brook trout) out of a total of 363 fish (89% brown trout and 12% brook trout) receiving marks. Most recaptured fish (87% of brown trout and 64% of brook trout) had mean trimonthly movements less than 75 m; 64% of recaptured brown trout and 39% of

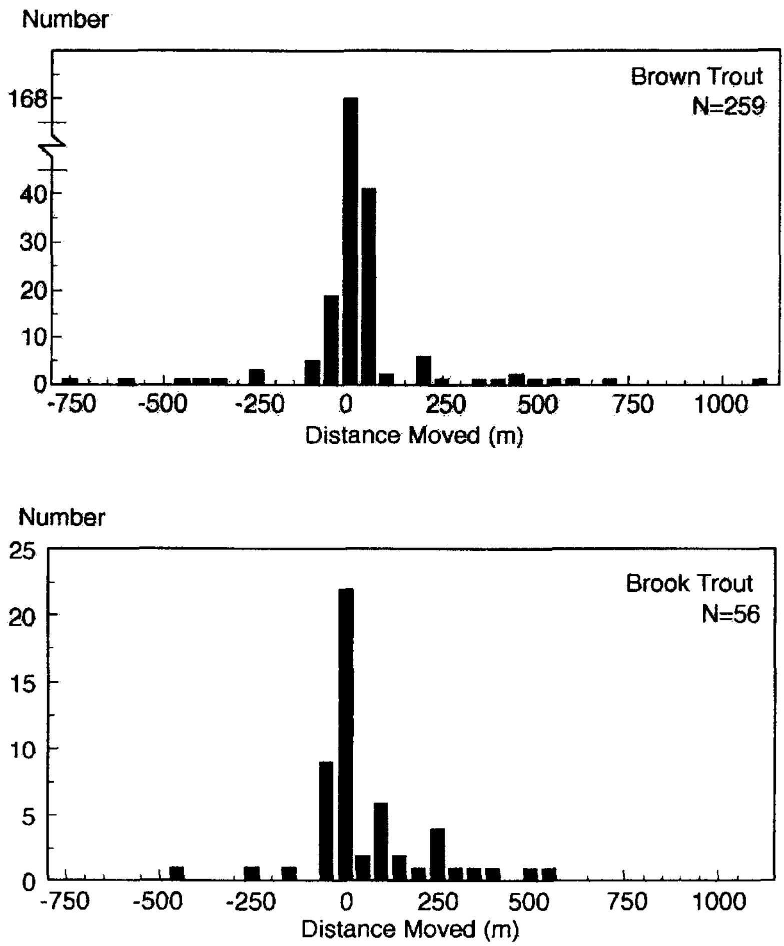

Figure 1. Mean trimonthly movements for brook trout and brown trout recaptured at least once during the study period.

recaptured brook trout stayed within one section of where they were first captured (Fig. 1). Overall mean trimonthly movement was 15 m upstream for brown trout and 27 m upstream for brook trout. The longest movement was 1,100 m upstream for brown trout and 550 m upstream for brook trout.

At the termination of the study, a 250-m stream segment below the lower study area boundary was electrofished to check for fish that had left the study area. This effort produced 1 marked brown trout immediately below the first section and 1 marked brook trout about 75 m below this section. A survey of the tributaries entering the study area produced only 1 marked brook trout out of 38 brook trout and 4 brown trout collected.

Growth and Production

Mean lengths of Laurel Fork brown trout at ages 1–3 were within the ranges reported for other populations (Table 1). Mean instantaneous growth rates for brown trout (Table 2) were highest in early fall (0.45 and 0.77), followed by early spring (0.41), early summer (0.18), and early winter (0.13). The high growth rates during early fall were greatly influenced by the growth of age-0 fish during those periods (1.29 in 1996 and 0.94 in 1997). Mean instantaneous growth rates for the entire population were significantly greater than zero for all sampling periods except early summer.

Like growth rate, production was highest in the early fall (3.44 kg/ha) followed by spring (2.48 kg/ha), summer (2.29 kg/ha), and winter (0.81 kg/ha) (Table 2). Early fall production was greatest because of a high growth rate and a large biomass. Though production paralleled growth rate, it did not decline as much as growth in early summer due to a greater biomass at that time. Total annual brown trout production in Laurel Fork was 9.02 kg/ha. The majority of this production (4.16 kg/ha or 46%) was by age-1 fish, though this was not significantly different from age-2 production (3.33 kg/ha or 37%). Production by older fish (age 3 and 4 combined) was 1.06 kg/ha (12%) and was not significantly different from age-0 production (0.47 kg/ha or 5%). The annual production to biomass ratio (P/B) for brown trout (0.85) was calculated as the mean biomass (10.6 kg/ha) divided by total annual production (9.02 kg/ha).

Table 1. Size (mm) at age for brown trout from different locales.

	Age			
Location	1	2	3	
Laurel Fork, Tenn.	112	184	268	(length in January)
East Tennessee streams	112	199	267	(back-calculated, Habera et al. 1999)
Poplar Creek, N.C.	105	182	240	(back-calculated, Coulston and Maughan 1981)
Jones Creek, Ga.	100	189	249	(back-calculated, Van Kirk 1969)
Chattooga River, Ga.	124	215	278	(back-calculated, Durniak 1989)
British Isles	102	175	221	(summarized, Carlander 1969)
Northeastern North America	173	229	287	(summarized, Carlander 1969)
Western North America	157	234	312	(summarized, Carlander 1969)

Table 2. Capture probability, density, instantaneous growth rates, biomass, and production (mean ± SE) for brown trout by age and 3-month sampling interval. Capture probability, density, and biomass are estimates at the beginning of the interval; instantaneous growth rate and production estimates are across the interval. Means in a column with the same letter are not significantly different (P<0.05).

Interval	Age	Capture probability	Density kg/ha	Instantaneous growth rate	Biomass kg/ha	Production kg/ha
Early fall[1] (Aug–Oct 1996)						
	0			1.29 ±0.15		
	1			0.40 ±0.04		
	2			0.07 ±0.08		
	3			0.77[2] ±0.12		
Total or mean[3]				0.77[a] ±0.12		
Early winter (Nov 1996–Jan 1997)						
	0		112 ±7	0.19 ±0.08	1.12 ±0.09	0.21 ±0.09
	1		65 ±4	0.10 ±0.03	3.30 ±0.25	0.33 ±0.09
	2		14 ±1	0.11[2] ±0.03	2.24 ±0.30	0.22 ±0.06
	3		2 ±1	0.11[2] ±0.03	0.50 ±0.04	0.05 ±0.04
Total or mean[3]		0.69[a,b] ±0.06	193[b] ±9	0.13[c] ±0.02	7.16[b] ±0.40	0.81[c] ±0.14
Early spring (Feb–Apr 1997)						
	1		56 ±4	0.76 ±0.04	0.77 ±0.07	0.59 ±0.06
	2		85 ±6	0.30 ±0.03	5.07 ±0.38	1.52 ±0.17
	3		6 ±1	0.30[2] ±0.03	1.23 ±0.12	0.37 ±0.05
Total or mean[3]		0.39[c] ±0.05	147[c] ±7	0.41[b] ±0.02	7.07[b] ±0.40	2.48[b] ±0.19
Early summer (May–Jul 1997)						
	1		120 ±8	0.36 ±0.04	3.48 ±0.27	1.25 ±0.17
	2		65 ±4	0.12 ±0.03	5.31 ±0.40	0.63 ±0.14
	3		11 ±1	0.12 ±0.90	2.21 ±0.22	0.27 ±0.63
	4		2 ±1	0.12[2] ±0.90	1.15 ±0.08	0.14 ±0.33
Total or mean[3]		0.56[b] ±0.05	198[b] ±14	0.18[b,c] ±0.10	12.15[a] ±0.53	2.29[a,b,c] ±0.75
Early fall (Aug–Oct 1997)						
	0		67 ±4	0.94 ±0.14	0.28 ±0.02	0.26 ±0.04
	1		134 ±7	0.34 ±0.02	5.79 ±0.36	1.99 ±0.17
	2		45 ±3	0.23 ±0.03	4.19 ±0.30	0.96 ±0.12
	3		5 ±1	0.23[2] ±0.03	0.99 ±0.13	0.23 ±0.04
Total or mean[3]		0.78[a] ±0.05	251[a] ±9	0.45[a,b] ±0.04	11.25[a] ±0.49	3.44[a] ±0.22

1. Density, biomass, and production could not be calculated for the first sample interval.

2. Instantaneous growth rates for the closest age class were used for age classes where sample sizes were small.

3. Total density, biomass, and production for all age classes; mean instantaneous growth rate for all age classes.

Discussion

Movement

Gowan et al. (1994) reviewed the literature on the movement of resident stream salmonids and concluded that the use of mark-recapture to evaluate movement results in a bias toward sedentary fish; trout that do not move tend to be recaptured whereas long-range movers often leave the study area and are never found. They maintained that authors focus on recaptures (the majority of which are usually found near where they were marked) and ignore the large number of fish never recaptured (often well over half), leading to the erroneous conclusion that stream salmonids are overwhelmingly sedentary. Gowan et al. (1994) conceded that many, even most, trout may be sedentary, but suggest that a significant minority moves, referring to their work with telemetry (Young 1994) and weirs to support their contention. We recaptured 87% of the fish we marked, a greater percentage than all but one (also 87%) of the 32 recapture studies reviewed by Gowan et al. (1994), suggesting we missed a few long-range movers. Further, our search downstream and in the tributaries for marked fish at the end of study resulted in only 2 fish and movements upstream were blocked.

Only 13% of recaptured brown trout in Laurel Fork moved more than 75 m. Therefore, even if most non-recaptured fish left the study area the total amount of movement would be less than that found by Young (1994) in Wyoming or Burrell (1997) in Georgia, where over half the brown trout monitored moved substantially. One explanation for the lack of brown trout movement in our study was their relatively small size. The vast majority of brown trout were <250 mm, which was the minimum size in the telemetry studies of Young (1994) and Burrell (1997). Young (1994) and Shetter (1968) found that larger brown trout moved more than smaller fish. Young (1994) and Burrell (1997) both noted that movement was strongly associated with fall spawning, but we did not observe movement associated with spawning. Besides involving larger fish, the studies of Young and Burrell were conducted in streams much larger that Laurel Fork. Clapp et al. (1990) and Meyers et al. (1992) found relatively long distance seasonal (summer/winter) migrations of brown trout, but again, these were large fish in large streams. It appears that movement of brown trout is often spawning movement of large fish in large streams and therefore was not pronounced in the small fish in Laurel Fork. Recaptured brook trout in our study moved more than brown trout (36% moved more than 75 m). If most of the non-recaptured brook trout moved, then the movement of brook trout in our study would have been similar to brook trout movement in a weir study by Gowan and Fausch (1996).

Growth and Production

Mean total length at age of Laurel Fork brown trout was very similar to other east Tennessee streams and slightly greater than other, similar-sized southern Appalachian streams (Poplar Creek, Jones Creek), but slightly less than the larger Chattooga River (Table 1). As a group, southern Appalachian brown trout were larger at age than those in the British Isles, but smaller than elsewhere in North America. Relatively small size has also been noted in southern Appalachian brook trout, and Laurel Fork brook trout were comparable in size at age to other reports from the region (Whitworth and Strange 1983, Konopacky and Estes 1986).

Growth rates and production of brown trout differed among sampling periods and ages. Low water temperature most likely caused early winter growth rates and production to be significantly lower than early spring and fall. Water temperatures are often near 0° C during January in southern Appalachian streams, limiting trout growth. Early spring and fall growth rates and production were higher than early summer, though not significantly so. Summer has been found to be a time of poor trout growth in the southern Appalachians due to a combination of warm temperatures and limited food (Coulston and Maughan 1981, Cada et al. 1987, Ensign et al. 1990). Age-0 fish had the highest growth rates for all periods for which they were present, but were second in production to age1 due to low biomass. Age-1 fish were second in growth rate to age 0, but had the highest production in 3 out of 4 sample periods. Older fish (ages 2 and 3) had the lowest rates of growth; during summer age 3 was not significantly greater than 0. Whitworth and Strange (1983) also found that age-1 fish dominated production in a brook and rainbow trout stream in Tennessee, although age 0 contributed little in that case.

Annual production for brown trout (9.02 kg/ha) in Laurel Fork was low. Although brook trout production is not included in this estimate, total salmonid production probably does not exceed brown trout production by more than 10% because of low brook trout biomass. Other production estimates for brown trout in the southeast are lacking, but brook and rainbow trout production have been found to range from 5 to 50 kg/ha in Tennessee and Virginia streams (Neves and Pardue 1983, Neves et al. 1985, Whitworth and Strange 1983). Kwak and Waters (1997) reviewed salmonid production estimates and found they ranged from 1 $\geq$ 500 kg/ha with estimates from southern Appalachian streams ranking among the lowest. Kwak and Waters (1997) reported a positive correlation between alkalinity and trout production up to an alkalinity of at least 200 mg/liter. The extremely soft water of Laurel Fork (mean alkalinity, 16.3 mg/liter) is typical of most southern Appalachian streams and probably explains the low production in the stream and region.

The production to biomass ratio (P/B) for Laurel Fork brown trout (0.85) was intermediate for P/B ratios reported from southern Appalachian streams. Neves and Pardue (1983) reported a P/B of 1.6 for brook trout in a Virginia stream, while Whitworth and Strange (1983) reported a P/B ratios of 0.96 for brook trout and 0.63 for rainbow trout from a Tennessee stream. P/B ratios for brown trout from Minnesota streams were reported to be about unity, but this relatively low ratio was attributed to the older ages classes (5–7) present, which were absent from Laurel Fork (Waters et al. 1990, Kwak and Waters 1997). The short life span of Laurel Fork brown trout (few live beyond age 3) is typical of other southern Appalachian brook and rainbow trout (Whitworth and Strange 1983, Larson and Moore 1985, Habera and Strange 1993).

The brown trout population in Laurel Fork can be characterized as small, young fish with slow growth and low annual production. These attributes are probably the result of low alkalinity resulting in a limited food supply. They show little evidence of the spawning or seasonal migrations often associated with brown trout populations, likely because of their small size and restricted stream habitat. One question that was not answered by our study was why Laurel Fork is dominated by brown trout to the exclusion of rainbow trout, an unusual circumstance in the southern Appalachians. It may be related to the fact that Laurel Fork has a relatively low gradient with a higher population of fine substrate (gravel and sand) than the typical high-gradient freestone southern Appalachian trout stream.

Management Implications

Clearly, the slow growth and low productivity in Laurel Fork result in brown trout that are small at age. The current 229-mm minimum size limit now in effect precludes most harvest since the vast majority of Laurel Fork's brown trout production is by fish smaller than that, and cumulative natural mortality becomes very high as fish approach the minimum size limit. We recommend that in situations like this, a lower minimum size limit, e.g., 178 mm would be more appropriate. This would make most age-2 and some age-1 brown trout legal for harvest and divert some of the natural mortality into the angler's creel.

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