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MANAGEMENT BRIEF

Recovery of Native Brook Trout Populations Following the Eradication of Nonnative Rainbow Trout in Southern Appalachian Mountains Streams

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Abstract

Nonnative Rainbow Trout *Oncorhynchus mykiss* have displaced native Brook Trout *Salvelinus fontinalis* in many southern Appalachian Mountains streams. We monitored the population recovery of Brook Trout following Rainbow Trout eradication at 10 sites in seven allopatric Rainbow Trout streams located in Great Smoky Mountains National Park, USA. Rainbow Trout were successfully eradicated by electrofishing or Fintrol (also known as antimycin-A), and Brook Trout were reintroduced at low densities (39–156 fish/km) from streams located within the park. Within 2 years after reintroduction, the density and biomass of adult Brook Trout recovered to levels comparable to the prerestoration density and biomass of Rainbow Trout. Spawning in the first autumn after reintroduction was assumed by the presence of young-of-the-year fish in seven out of nine sites surveyed during the following summer. Brook Trout density and biomass 3–5 years after restoration did not significantly differ from those in natural allopatric populations within the park in young-of-the-year fish but were significantly lower in adults. Individual body size of adult and young-of-the-year fish were density dependent after restoration, indicating that Brook Trout populations had recovered to a point that habitat saturation triggered intraspecific competition. We conclude that Rainbow Trout removal has been a viable management technique to restore Brook Trout populations in the park.

Introductions of fish species are widespread in freshwater habitats and have impacted native species and ecosystems (Gozlan et al. 2010). Introduced species are the second most important cause, after habitat loss and degradation, for known freshwater fish extinctions (Miller et al. 1989). Native to western North America, Rainbow Trout *Oncorhynchus mykiss* have been widely introduced for recreational fisheries and have established populations globally in regions that harbor suitable habitats (Fausch et al. 2001). Rainbow Trout affect native aquatic species via several mechanisms such as competition and hybridization (e.g., Hitt et al. 2003; Baxter et al. 2004; Thibault and Dodson 2013).

There are approximately 71 species of fish native to Great Smoky Mountains National Park (GRSM), including Brook Trout *Salvelinus fontinalis* (King 1937; Kulp and Moore 2000). Brook Trout were once prolific in park streams down to an elevation of roughly 400 m (Powers 1929; King 1937) and were sought as an important food source and leisurely as a magnificent sport fish (King 1938). Introductions of Rainbow Trout began after the turn of the century (circa 1910) in GRSM to meet the demand for increased angling opportunities, and the establishment of Rainbow Trout populations coincided with declines of native Brook populations (King 1938; Larson and Moore 1985). Brook Trout have been extirpated in approximately 75% of the historical range within GRSM since 1900. The presence of Rainbow Trout, along with logging and water quality degradation prior to park establishment in 1934, is considered a major cause of Brook Trout population decline

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within GRSM (Habera and Moore 2005; Habera et al. 2010). Today, allopatric Brook Trout populations are limited to headwater reaches higher than 914 m above sea level in GRSM, and Rainbow Trout occupy downstream reaches that were historically occupied by Brook Trout (Larson and Moore 1985).

National Park Service (NPS) policy is unique among land management agencies in that the NPS is mandated to protect and preserve “naturally functioning ecosystems,” which includes the removal of nonnative species (NPS 2006). Given the negative impacts on native Brook Trout, in the late 1950s, the U.S. Fish and Wildlife Service and NPS began taking steps to remove nonnative Rainbow Trout from park streams in order to restore Brook Trout back to portions of their former range (Lennon and Parker 1959). Rainbow Trout removal techniques have included angling (Larson et al. 1986; Moore et al. 1986), annual removals using backpack electrofishing gear (Moore et al. 1986; West et al. 1990), and the use of piscicides such as rotenone, cresol, and Fintrol (also known as antimycin-A; Lennon and Parker 1959; Moore et al. 2005; Vinson et al. 2010). Although these studies compared the feasibility of various Rainbow Trout eradication techniques, it is similarly important to evaluate the recovery of Brook Trout populations in response to Rainbow Trout removals. A quick and full Brook Trout population recovery in GRSM would help achieve two important mandates of the NPS, namely ecological conservation and recreational use of park resources (i.e., angling opportunities; Kulp and Moore 2005).

In this paper, we evaluated the recovery of Brook Trout populations following successful Rainbow Trout eradication and subsequent Brook Trout translocation from neighboring streams in GRSM. We analyzed three-pass electrofishing data collected before and after restoration at 10 sites in seven formerly allopatric Rainbow Trout streams. The recovery of Brook Trout populations was evaluated based on the following three criteria. First, density and biomass of Brook Trout young-of-the-year (age 0) and adult individuals during postrestoration years were compared with those of prerestoration Rainbow Trout populations. Because Rainbow Trout were completely removed and never reinvaded the restored sites in this study, we considered that this before-and-after assessment would provide the most direct measure of population recovery. Second, density and biomass of Brook Trout in restored streams were compared with those in other naturally allopatric Brook Trout streams within the park. We posited that these allopatric populations represent the best available conditions against which to compare the recovery of restored populations. Finally, we examined a density-dependent effect on age-0 and adult body size in Brook Trout. We assumed that the presence of density-dependent body size would indicate intraspecific competition (Lobón-Cerviá 2007; Grossman et al. 2010), and such a sign of resource limitation would indicate that populations have recovered to a point near carrying capacity of the habitat.

METHODS

Study area and restoration history.—Great Smoky Mountains National Park was established in 1934 and currently encompasses 211,040 ha of southern Appalachian hardwood forests in eastern Tennessee and western North Carolina. The park includes more than 4,640 km of streams in 45 major watersheds (>5 km^2), all of which eventually flow into the Tennessee River. They range from first- to sixth-order in stream size and include both coldwater and coolwater streams.

The U.S. Fish and Wildlife Service (which managed the fisheries within GRSM until 1984) and NPS began removing Rainbow Trout from select streams in the late 1950s (Lennon and Parker 1959) using angling (Larson et al. 1986; Moore et al. 1986), backpack electrofishing (Moore et al. 1986; West et al. 1990), and rotenone and cresol (Lennon and Parker 1959). The degree of success varied among these efforts depending on the presence of sufficient physical barriers to nonnative fish reinvasion and the completeness of removal of nonnative target species (Moore et al. 1986; West et al. 1990). A plan for posttreatment monitoring of restored Brook Trout populations was not in place during these initial efforts. Only two Brook Trout restoration attempts in the 1980s were successful (West et al. 1990).

The NPS restored six GRSM streams successfully in the early 1990s using single and multiple electrofishing removals (Kulp and Moore 2000). In 2000, GRSM completed a programmatic environmental assessment identifying six additional streams that met GRSM restoration criteria (e.g., sufficient barrier to reinvasion, previous record[s] of Brook Trout occurrence, and target stream segment of feasible size) for Brook Trout restoration using the pesticide Fintrol (Moore at al. 2005). Since 2001, three of these six streams have been treated with Fintrol (Moore et al. 2005; Vinson et al. 2010; Gibbs et al. 2015). Annual population monitoring was conducted before and after restoration, and angling was prohibited for 3–4 years after restoration to facilitate population recoveries. In this paper, we analyze monitoring data from seven restored streams for which at least 1 year (range = 1–11 years) of pretreatment Rainbow Trout data and at least 2 years (range = 2–5 years) of posttreatment Brook Trout data within 5 years after treatment were available (Table 1; Figure 1).

The seven study streams were functionally allopatric Rainbow Trout streams prior to restoration. Brook Trout individuals were absent in all streams, except that small sympatric Brook Trout populations existed in short extreme headwaters of Lynn Camp Prong (380 m) and Sams Creek (730 m) at densities ranging from 6 to 13 fish/100 m^2 (Table 1; Figure 1). Rainbow Trout were removed using multiple electrofishing treatments at four streams and Fintrol at three streams (Table 1). Electrofishing removals consisted of four to five three-pass depletion efforts within 1 year (June–September and the following May–June) using backpack electrofishing units (Kulp and Moore 2000). Block nets were deployed at

TABLE 1. A list of study streams in which Brook Trout were translocated after a Rainbow Trout eradication. Year restored indicates the year in which Rainbow Trout were removed and Brook Trout were translocated.

Stream	Year restored	Rainbow Trout removal method	Elevation range (m)	Site ID[a]	Restored stream length (km)	Number of Brook Trout reintroduced	Number of years of Rainbow Trout survey[b]	Number of years of Brook Trout survey[c]
Ash Camp Branch	2000	Multiple electrofishing	1,012–1,091	4	0.86	75	1	5
Bear Creek	2003	Fintrol	605–1,064	18, 33	5.60	220 (2004), 250 (2006)	1	3
Leconte Creek	1999	Multiple electrofishing	604–1,012	1	2.70	320	3	4
Lynn Camp Prong	2008	Fintrol	617–1183	11, 33	15.90	2,007	2	4 (site 11) 3 (site 33)
Mannis Branch	1996	Multiple electrofishing	597–677	8	0.86	105	1	4
Sams Creek	2001	Fintrol	658–1,146	3, 5	4.80	480	11	4 (site 3) 5 (site 5)
Winding Stair Branch	2001	Multiple electrofishing	799–1,000	4	1.60	75	2	2

[a] Up to two sites were used in each stream and they were separated by >800 m from each other to ensure demographic independence.

[b] Rainbow Trout surveys were conducted before and during year of restoration in each stream.

[c] Number of Brook Trout surveys conducted within 5 years after restoration.

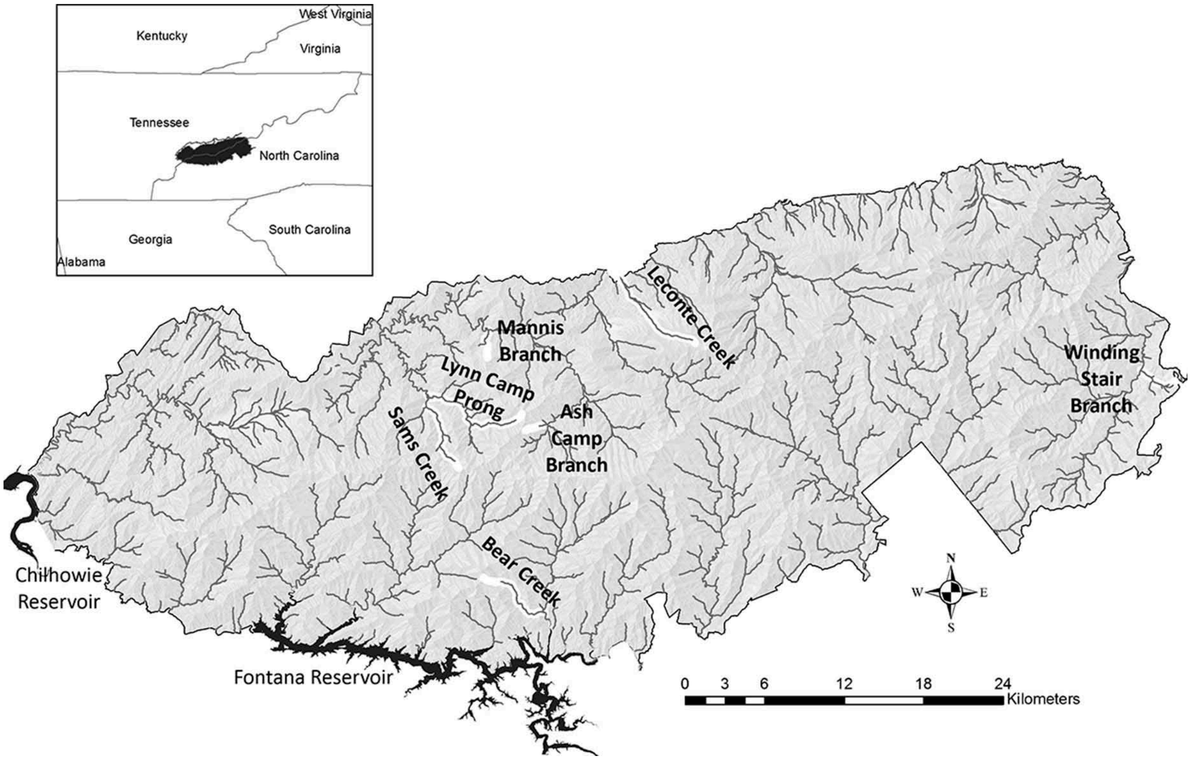

FIGURE 1. A map of GRSM identifying seven study streams (white lines) where Rainbow Trout were completely eradicated and translocated Brook Trout populations were monitored.

upper and lower stream sections prior to electrofishing removal efforts, similar to Habera et al. (1996). Initial removals typically removed a majority of the larger fish (150–300 mm TL), with subsequent removals of the subadults (100–125 mm TL) and age-0 fish. Fintrol was applied to a stream at a concentration of 8 parts per billion (ppb) for 8 h using a Farnum float system attached to a 19-L bucket (Moore et al. 2005). A series of fish holding cages were placed along the stream just above every treater to ensure that an 8-ppb Fintrol concentration was maintained, resulting in 100% mortality rates in each cage from one treater to the next. Fluorescine dye was applied at the most upstream station, and successive downstream stations were turned on when the dye flume reached that station. Rainbow Trout were completely eradicated after electrofishing and Fintrol methods in all streams, except in upper Sams Creek where three Rainbow Trout individuals (160–186 mm TL) were detected and euthanized in a follow-up survey 1 year after the Fintrol treatment. No Rainbow Trout were observed in Sams Creek after that point.

Following complete Rainbow Trout eradications at seven study streams, Brook Trout individuals were collected from streams within the closest major drainages that were characterized with pure Southern Appalachian genotypes and translocated into the restored stream segment (Kulp and Moore 2000; Moore et al. 2005). Both age-0 and adult fish were used in translocations depending on availability and translocation densities ranging from 39 to 156 fish/km or 1.00 to 3.63 fish/100 m^2 (Table 1). Translocation density values were low relative to densities observed in wild trout streams within GRSM (see Results). Target translocation densities of Brook Trout have been less than 125 fish/km based upon experience in other restoration projects in GRSM, and its rationale was to minimize potential demographic and genetic impacts on source populations, which were not always large in size.

Field survey.—In each stream, 100-m sample sites were established from a physical barrier to the upstream distribution limit of invaded Rainbow Trout populations. Sample sites were numbered with metal tags starting at the barrier, and tags were then placed on trees every 100 m upstream until they surpassed the end of the Rainbow Trout distribution. Tributaries containing Rainbow Trout were numbered similarly starting at their confluence with the main stem. Once sites were established, one to two sites were randomly selected for monitoring within every 1 km of treatment area. Pre- and posttreatment monitoring surveys occurred between May and September during base flow conditions. In this study, data from one or two sites were used per stream (Table 1), and sites were separated by at least 800 m from each other to ensure demographic independence when two sites were used in a stream.

Pre- and posttreatment density and biomass were determined using three-pass depletion surveys in 100-m sites

TABLE 2. Mean values (SE) of chemical and physical characteristics of pre- and posttreatment monitoring sites in Brook Trout restoration streams. Field measurements were taken between May and September.

Stream	Stream order	Conductivity (μS/cm)	Temperature (°C)	Discharge (m^3/s)	Watershed area (km^2)	Mean width (m)	Stream gradient (%)
Ash Camp Branch	2	15.3 (0.9)	14.1 (0.4)	0.040 (0.005)	1.70	3.3 (0.2)	14.1
Bear Creek	2	12.0 (0.3)	16.2 (0.4)	0.084 (0.018)	8.44	3.9 (0.2)	7.1
Leconte Creek	2	15.8 (0.5)	16.3 (0.3)	0.084 (0.013)	5.78	4.7 (0.2)	8.5
Lynn Camp Prong	3	13.1 (0.4)	17.3 (0.3)	0.101 (0.026)	30.97	9.7 (0.8)	2.9
Mannis Branch	2	14.7 (0.7)	16.0 (0.4)	0.017 (0.006)	3.19	3.4 (0.1)	5.8
Sams Creek	3	11.8 (0.6)	14.9 (0.3)	0.117 (0.022)	10.80	6.9 (0.3)	7.2
Winding Stair Branch	3	23.5 (2.0)	14.3 (0.6)	0.021 (0.002)	5.64	4.0 (0.3)	6.9

using the backpack electrofishing techniques outlined in Habera et al. (1996). Block nets (6–10-mm bar mesh) were used to close the lower and upper end of each 100-m site. Pool depth in each sample site was less than 1 m, and sites did not contain complex habitat that could reduce capture efficiency (Habera et al. 1992, 2010). Upon completion of an electrofishing pass, total length (mm) and weight (g) were recorded for each individual by species, and the fish were held in holding cages outside of the site until the depletion survey was complete. All fish were then released back in the site of original capture, except when the survey was intended for Rainbow Trout removals (Habera et al. 1996). Chemical and physical stream characteristics data were collected during each sampling event (Table 2). Study sites were small in size (stream order: second or third) and characterized with sequences of pools and riffles (Table 2).

Statistical analysis.—A length-frequency histogram was plotted for each survey occasion to distinguish age-0 from adult (>1 year old) individuals. Abundance of each size-class was estimated using the Burnham maximum likelihood estimator in the Microfish 3.0 software (Van Deventer and Platts 1989). The population estimate was converted to number of fish per 100 m^2, and biomass was calculated as total mass weight of individuals per hectare (kg/ha), based upon 10 stream width measurements taken every 10 m at the site.

Density and biomass of Brook Trout age 0 and adults during 5 years after reintroduction were compared with those of Rainbow Trout before their eradication. This was the only before-and-after comparison possible because formerly allopatric Rainbow Trout streams were targeted for restoration, and Rainbow Trout individuals were completely eradicated without any subsequent reinvasion in all streams. An ANOVA was conducted by specifying stream sites and years before and after reintroduction as fixed effects, with the primary focus on comparing prerestoration Rainbow Trout values with postrestoration Brook Trout values in each of the five postrestoration years. Age-0 and adult density and biomass of Brook Trout were divided by mean prerestoration Rainbow Trout density and biomass at each site to calculate percent recovery in each year. Percent recovery values were log transformed (i.e., $\log_{10}$[percent recovery + 1]) to improve normality prior to analysis. Statistical significance was set at $\alpha = 0.05$ level in the ANOVA and all other analyses in this paper. When statistical significance of the year effect was declared in the ANOVA, we conducted a follow-up Tukey's honest significance test to determine which years differed in density or biomass.

Brook Trout density and biomass at restored sites were also compared with those at naturally allopatric Brook Trout sites in GRSM. Density and biomass data 1–2 years after restoration were not included to account for the recovery period immediately following reintroduction (see Results). Naturally allopatric Brook Trout data included those streams surveyed using the same protocol between 1997 and 2014. We used data starting in 1997 because this was the year in which the first postrestoration survey was conducted in our study streams (i.e., Mannis Branch; Table 1). Age-0 and adult Brook Trout density and biomass were compared between restored sites and naturally allopatric sites using a *t*-test. A total of 46 samples were available at 10 sites from seven restored streams, versus 317 samples at 51 sites from 25 naturally allopatric streams. Restored and allopatric streams were similar in stream habitat characteristics (Table 3), but stream temperatures at allopatric streams were significantly colder than those at restored sites (*t*-value = –2.19, df = 14.34, *P* = 0.04).

Density-dependent effect on individual body size was examined for age 0 and adults. For each size-class, individual TL (mm) was used as a response variable in linear mixed-effect models. We hypothesized that individual body size might be affected by day of year of sampling (particularly for age 0) as well as density. These two predictor variables, standardized by their mean values, were treated as fixed effects, and site and year were treated as random effects in mixed models to account for unexplained spatial and temporal variation. Mixed models were fit using lmerTest package in Program R, and all other statistical analyses were also conducted in R (R Development Core Team 2014). For this

TABLE 3. Median (minimum, maximum) value of habitat variables in restored (n = 7) versus naturally allopatric Brook Trout streams (n = 25).

	Restored streams	Allopatric streams
Conductivity (µS/cm)	14.7 (11.8, 23.5)	15.1 (5.0, 27.2)
Temperature (°C)	16.0 (14.1, 17.3)	14.3 (11.0, 17.3)
Discharge (m^3/s)	0.084 (0.017, 0.117)	0.070 (0.024, 0.261)
Width (m)	4.0 (3.3, 9.7)	4.3 (3.1, 7.7)
Gradient (%)	7.1 (2.9, 14.1)	9.1 (2.1, 14.5)

analysis, we used all posttranslocation data available at study sites because restricting years of analysis within 5 years after restoration might encompass only the initial recovery period and mask the presence of a density-dependent effect on body size. Three to 16 years of data (mean = 6 years) were available for each site.

RESULTS

Brook Trout density and biomass recovered quickly to a level comparable to prerestoration Rainbow Trout density and biomass (Figure 2). There was no statistically significant temporal difference between prerestoration Rainbow Trout age 0 and postrestoration Brook Trout age 0 in density (ANOVA: F = 1.10, df =5, P = 0.39) and biomass (ANOVA: F = 0.62, df =5, P = 0.68; Figure 2). Age-0 individuals were observed in seven out of nine sites surveyed 1 year following restoration, indicating that fish translocated during summer spawned later in that autumn at most sites. Brook Trout age-0 abundance increased over time at restored sites; the median percent recovery in age-0 density across sites was 13% in the first year after restoration, 36% in the second year, 121% in the third year, 172% in the fourth year, and 263% in the fifth year (Figure 2). The recovery of adult Brook Trout was slower than that of age 0, but their density and biomass were again comparable to that of Rainbow Trout before restoration in just 2 years after reintroduction (Figure 2). Adult density differed significantly among years (ANOVA: F = 2.53, df = 5, P < 0.05), and among-year variation was nearly significant in biomass (ANOVA: F = 2.44, df =5, P = 0.06). Statistical significance in adult density was due to the difference between the prerestoration Rainbow Trout period and the first-year Brook Trout density after reintroduction (Tukey's test: P = 0.05). Adult density and biomass of Brook Trout during years 2–5 after reintroduction were not statistically different from prerestoration Rainbow Trout values (Tukey's test: P > 0.56). The median percent recovery in adult density across sites was 10% in the first year after restoration, 69% in the second year, 62% in the third year, 44% in the fourth year, and 74% in the fifth year (Figure 2).

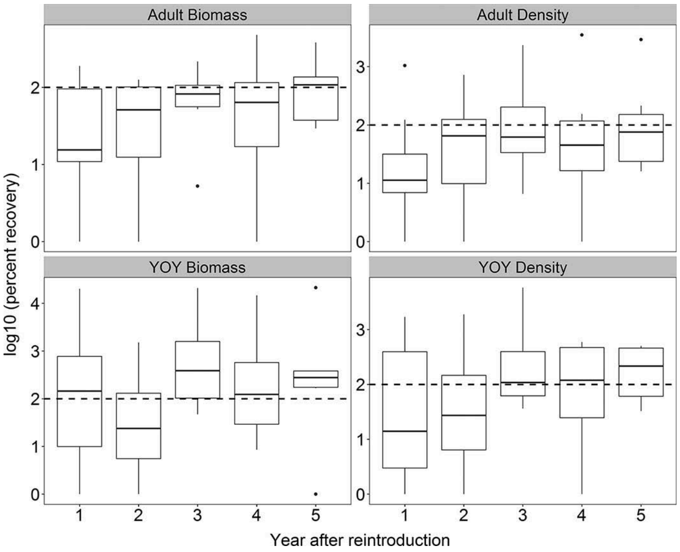

FIGURE 2. Annual percent recovery ($\log_{10}$) of Brook Trout density (number/100 m^2) and biomass (kg/ha) of adults and age 0 (YOY) across study sites, relative to Rainbow Trout density and biomass prior to restoration. Prerestoration Rainbow Trout level is indicated by the dashed horizontal line (i.e., 100% recovery or $\log_{10}[100] = 2$). Boxes show the interquartile ranges with medians represented by horizontal lines. Whiskers extend 1.5 × IQR (interquartile range) from lower and upper ends of boxes, and filled circles indicate outliers.

There was no statistically significant difference between restored sites and naturally allopatric Brook Trout sites in age-0 density (t = 1.79, df = 81.63, P = 0.08) and biomass (t = 1.76, df = 344.32, P = 0.08; Figure 3). Mean Brook Trout age-0 density was 6.40 fish/100 m^2 at restored sites (SD = 5.19, n = 46) and 8.00 at naturally allopatric sites (SD = 8.20, n = 317). Mean Brook Trout age-0 biomass was 1.83 kg/ha at restored sites (SD = 1.48, n = 46) versus 3.52 at allopatric sites (SD = 16.59, n = 317). There was a statistically significant difference between restored and allopatric sites in adult density (t = 8.25, df = 152.12, P < 0.001) and biomass (t = 6.99, df = 123, P < 0.001). Mean adult density was 5.19 fish/100 m^2 at restored sites (SD = 3.98, n = 46) and 11.94 at allopatric sites (SD = 10.33, n =317), and mean adult biomass was 15.04 kg/ha (SD = 8.93, n = 46) at the former sites and 27.08 (SD = 20.03, n = 317) at the latter sites (Figure 3).

Trout body size was negatively related to density in both age 0 (Figure 4) and adults (Figure 5). Sampling day of year affected age-0 body size (slope coefficient = 7.00, t = 20.40, P

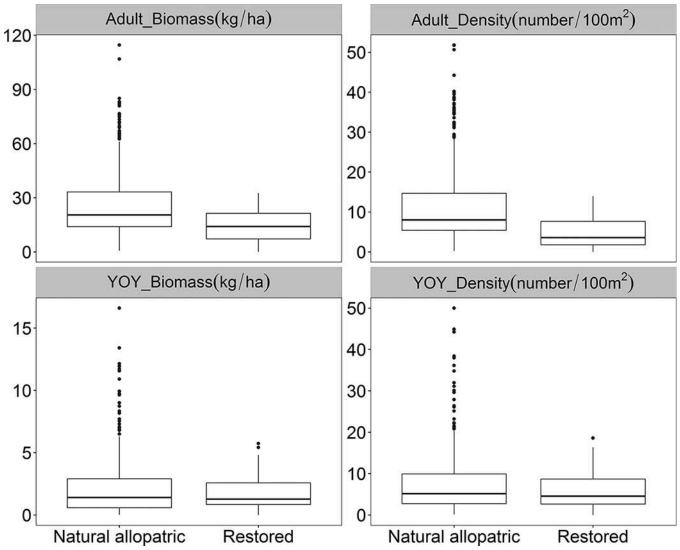

FIGURE 3. Comparison of adult and age-0 (YOY) density (number/100 m^2) and biomass (kg/ha) at naturally allopatric Brook Trout sites (n = 317 samples at 10 sites) and restored Brook Trout sites (n = 46 samples at 51 sites). Boxes show the interquartile ranges with medians represented by horizontal lines. Whiskers extend 1.5 × IQR (interquartile range) from lower and upper ends of boxes, and filled circles indicate outliers.

< 0.001) more strongly than density (slope = –1.38, t = –5.04, P < 0.001). Site random effect (SD = 5.33) was larger than year random effect (SD = 3.94). To the contrary, density was the more important predictor of adult body size (slope = –8.14, t = –7.65, P < 0.001) than sampling day of year (slope = –5.411, t = –4.40, P < 0.001). Site random effect (SD = 14.40) was again larger than year random effect (SD = 10.64) in adults.

DISCUSSION

Negative impacts of nonnative salmonids on native salmonids have been documented in the laboratory (Taniguchi et al. 1998; McHugh and Budy 2005) and field (Nakano et al. 1998; McGrath and Lewis 2007). Removals of nonnative salmonids are consequently assumed to lead to positive effects on native salmonids, but population-level benefits in natural settings have rarely been confirmed. In addition, a major focus of nonnative salmonid controls has been to determine effective methods of removals (Moore et al. 1986; Kulp and Moore 2000; Meyer et al. 2006), and population recoveries of native salmonids after nonnative removals have been investigated much less frequently (Peterson et al. 2004; Hoxmeier and Dieterman 2016). Our study provides a unique insight into population recoveries of native Brook Trout after a complete eradication of nonnative Rainbow Trout using long-term data sets collected at multiple streams.

Brook Trout abundance and biomass recovered quickly to the prerestoration Rainbow Trout level. Evidence of successful spawning of Brook Trout during the first autumn following translocation was determined by the presence of age-0 individuals at seven out of nine sites. The immediate reproduction resulted in age-0 Brook Trout density and biomass that were comparable to or above the prerestoration age-0 Rainbow Trout level in just 1 year after adult reintroduction. The abundance of age-0 Brook Trout is strongly affected by density-independent (environmental) factors (Kanno et al. 2016), and high age-0 recruitment can result from low spawner abundance in salmonids (Milner et al. 2003; Lobón-Cerviá 2009). We consider that high fecundity and suitable spawning habitat were responsible for a quick and full recovery of age-0 individuals. In addition, adult Brook Trout density and biomass did not statistically differ from the prerestoration Rainbow Trout level except for the first year after restoration. This decrease in adult Brook Trout numbers should be expected because many translocated individuals were adults. Due to food limitation associated with low productivity waters (Ensign et al. 1990), Brook Trout and Rainbow Trout in southern Appalachian Mountains streams are short lived (≤4 years old; Kulp and Moore 2005), and a small number of age-0 individuals used during translocations would result in a small adult population size in 1 year after reintroduction. The quick recovery of Brook Trout populations in this study is similar to that in a few other studies assessing native trout population recoveries following nonnative trout removals or reductions (Peterson et al. 2004; Hoxmeier and Dieterman 2016).

Although statistically not significant, population size structure tended to shift between prerestoration Rainbow Trout and postrestoration Brook Trout. Specifically, more age 0 and fewer adults were present in Brook Trout populations relative to prerestoration Rainbow Trout populations. The slight decrease in adult Brook Trout density and biomass relative to those of prerestoration Rainbow Trout follows the findings of Benjamin and Baxter (2010, 2012), who reported reduced density and production of native trout versus nonnative trout.

Brook trout biomass and density were comparable between restored sites and naturally allopatric sites. Age-0 biomass and density were not statistically different between the two groups. Adult biomass and density were statistically higher in naturally allopatric sites. However, the range of biomass and density values overlapped greatly between restored and naturally allopatric sites (Figure 3), and statistical significance is partly due to a large sample size (n = 46 for restored samples and n = 317 for naturally allopatric samples). Naturally allopatric sites also included some of the best Brook Trout streams within GRSM located in colder headwater streams (Table 3), whereas restored sites were located further downstream.

Body size of age-0 and adult Brook Trout was density dependent. Density-dependent body size has been commonly reported in stream salmonid populations across life stages (Utz and Hartman 2009; Grossman et al. 2010; Baerum et al. 2013; Lindeman et al. 2015). Sampling day of year was a more

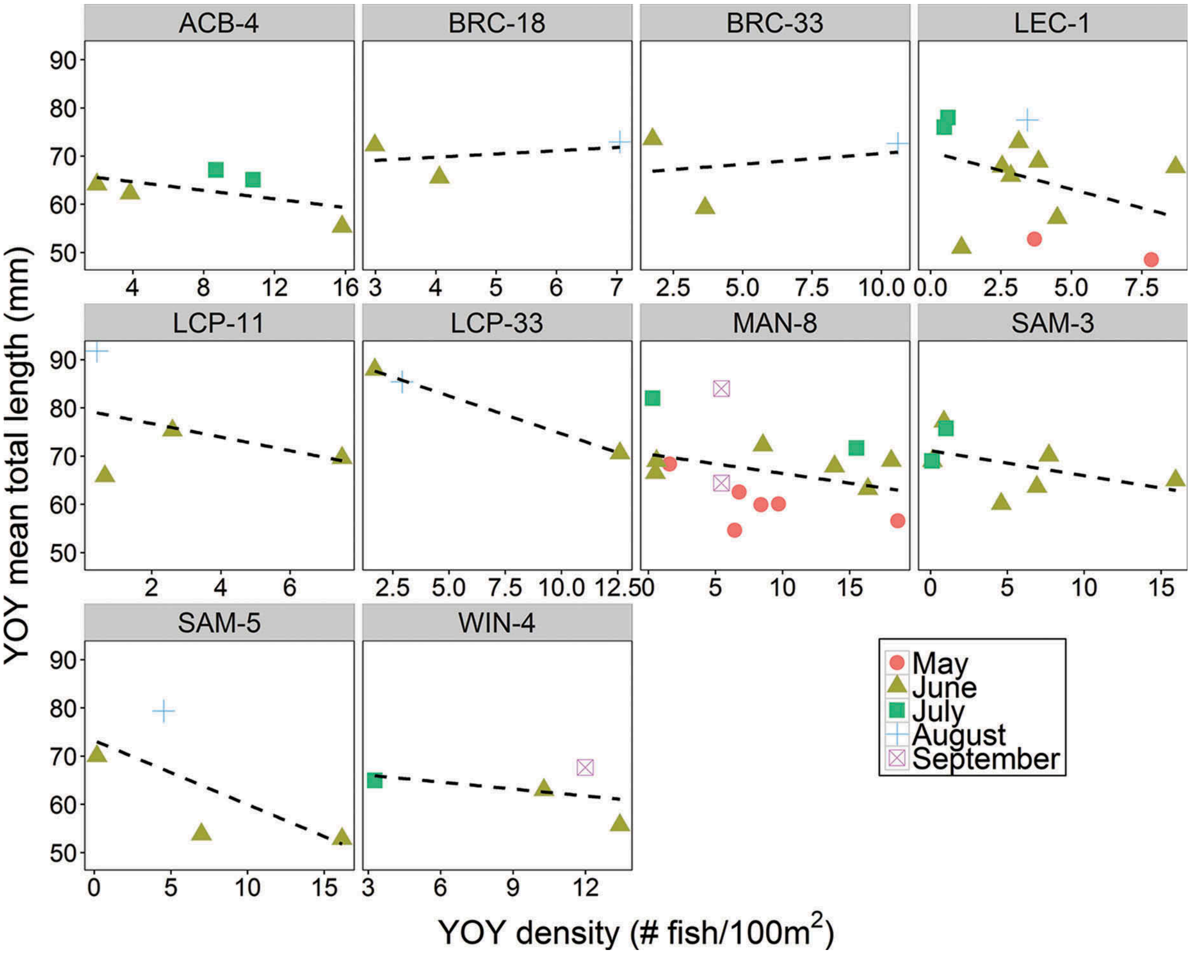

FIGURE 4. Relationships between age-0 (YOY) density and mean TL across years at 10 study sites. A dotted linear line indicates simple linear regression line fit for each site. Points were denoted by month to visualize the effect of sampling timing on mean TL. Site abbreviations are ACB-4 (Ash Camp Branch site 4), BRC-18 (Bear Creek site 18), BRC-33 (Bear Creek site 33), LEC-1 (Leconte Creek site 1), LCP-11 (Lynn Camp Prong site 11), LCP-33 (Lynn Camp Prong site 33), MAN-8 (Mannis Branch site 8), SAM-3 (Sams Creek site 3), SAM-5 (Sams Creek site 5), and WIN-4 (Winding Stair Branch site 4).

important factor than density for age-0 body size, and this result is plausible because age-0 individuals hatch in late winter and our sampling period (May–September) covered their growing season. The evidence of density-dependent body size indicated that intraspecific competition resulted in resource competition (i.e., habitat saturation).

Based on these results, we conclude that the Rainbow Trout removal has been a viable management technique to restore Brook Trout populations within GRSM. Brook Trout biomass and density were temporally comparable to prerestoration Rainbow Trout values and spatially comparable to existing natural allopatric Brook Trout populations for age-0 individuals, and density-dependent effect on body size was observed. Adult biomass and density at restored sites remained low relative to natural allopatric sites, but it was the only criterion that indicated a partial recovery among an otherwise full and quick recovery of restored populations. Since 1981, the NPS has restored 32.32 km of Brook Trout populations at seven study streams (Table 1) as well as 11.84 km at four other streams within GRSM, for a total of 44.16 km (at the time of this writing in 2016). Monitoring efforts were invaluable in evaluating the experimental Rainbow Trout removal for the benefit of native Brook Trout. Based upon the recovery of restored Brook Trout populations and another study that indicated that legal angling posed no negative population-level effects on wild trout (Kulp and Moore 2005), GRSM reopened fishing and harvest of Brook Trout parkwide in 2006. Our study documents that potential Brook Trout habitat is currently occupied by Rainbow Trout within the park and the presence of the nonnative trout species is a threat to conservation of the native trout, but Brook Trout populations can be restored in their historic habitat by facilitating the removal of Rainbow Trout populations.

We consider that a couple of factors were critical in successful Brook Trout recoveries in this study. First, Rainbow Trout individuals were completely eradicated from all study

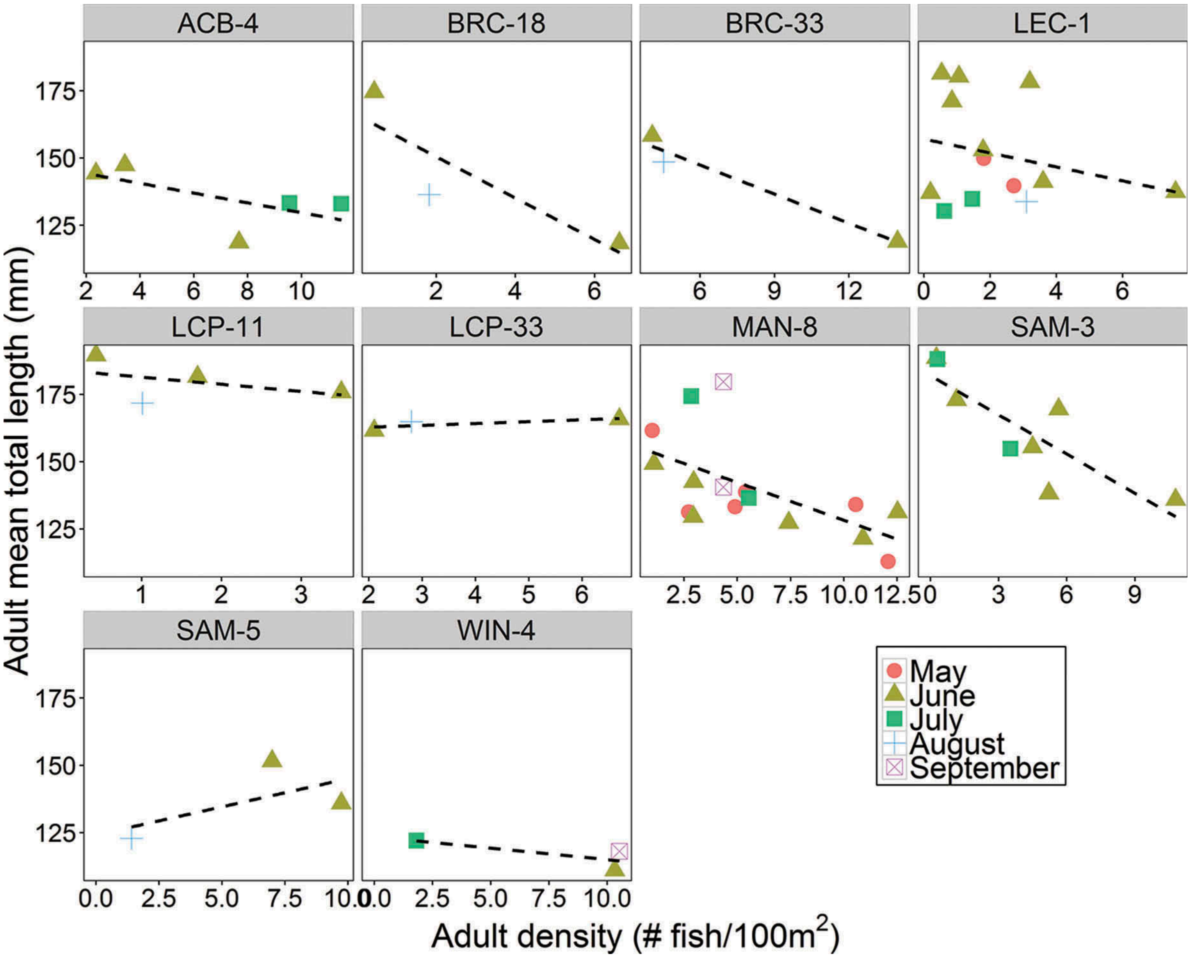

FIGURE 5. Relationships between adult density and mean TL across years at 10 study sites. A dotted linear line indicates simple linear regression line fit for each site. Points were denoted by month to visualize the effect of sampling timing on mean TL. See Figure 4 caption for site abbreviations.

sites, which is essential in order to successfully establish an allopatric Brook Trout population (West et al. 1990). Both electrofishing and Fintrol methods were highly effective in our small headwater streams that were isolated above physical barriers and lacking complex habitat structures. This aspect is unique because many studies can typically reduce, but not eradicate, target trout species (Peterson et al. 2004; Meyer et al. 2006; Hoxmeier and Dieterman 2016). Second, study streams were located in a national park and were protected from current anthropogenic activities. Restored sites did not differ in most habitat characteristics from naturally allopatric Brook Trout sites within GRSM (Table 3). This provided a favorable setting for successful Brook Trout recoveries, although habitat loss and fragmentation is widely recognized a key factor that has contributed to the rangewide decline of Brook Trout (DeWeber and Wagner 2015).

As climate and land use change is projected to affect remaining Brook Trout populations further (Flebbe et al. 2006; DeWeber and Wagner 2015), Rainbow Trout removal can be an increasingly important management technique. Great Smoky National Park was uniquely able to implement this management technique, but it may not be universally applicable to other potential Brook Trout streams based on cultural and social considerations (e.g., angler opposition). Nonnative salmonids can establish a higher population size than native salmonids (Benjamin and Baxter 2010), and nonnative trout removal may not be feasible when a robust population has already been established and is known among anglers. Brook Trout restoration also needs to take into account biological factors. Specifically, the optimal numbers and sources of Brook Trout individuals that are used for reintroduction have not received rigorous scrutiny, but they are important in maintaining genetic diversity at restored populations and minimizing demographic and genetic impacts on source populations. Posttranslocation genetic monitoring of the newly established population would be useful for ensuring representation and retention of genetic diversity from source populations and for determining the need for additional translocation when allelic diversity is low (Whiteley et al. 2015). In any case, existing and future Brook Trout restoration projects should incorporate a monitoring component to track population recovery.

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REFERENCES

Baerum, K. M., T. O. Haugen, P. Kiffney, E. M. Olsen, and L. A. Vøllestad. 2013. Interacting effects of temperature and density on individual growth performance in a wild population of Brown Trout. Freshwater Biology 58:1329–1339.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85:2656–63.

Benjamin, J. R., and C. V. Baxter. 2010. Do nonnative salmonines exhibit greater density and production than the natives they replace? A comparison of nonnative Brook Trout with native Cutthroat Trout. Transactions of the American Fisheries Society 139:641–651.

Benjamin, J. R., and C. V. Baxter. 2012. Is a trout a trout? A range-wide comparison shows nonnative Brook Trout exhibit greater density, biomass, and production than native inland Cutthroat Trout. Biological Invasions 14:1865–1879.

DeWeber, J. T., and T. Wagner. 2015. Predicting Brook Trout occurrence in stream reaches throughout their native range in the eastern United States. Transactions of the American Fisheries Society 144:11–24.

Ensign, W. E., R. J. Strange, and S. E. Moore. 1990. Summer food limitation reduces Brook and Rainbow trout biomass in a southern Appalachian stream. Transactions of the American Fisheries Society 119:894–901.

Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. R. Townsend. 2001. Flood disturbance regimes influence Rainbow Trout invasion success among five Holarctic regions. Ecological Applications 11:1438–55.

Flebbe, P. A., L. D. Roghair, and J. L. Bruggink. 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. Transactions of the American Fisheries Society 135:1371–82.

Gibbs, W. K., M. A. Kulp, S. E. Moore, and S. B. Cook. 2015. Effects of antimycin and its neutralizing agent, potassium permanganate, on aquatic macroinvertebrates in a Great Smoky Mountains National Park watershed. North American Journal of Fisheries Management 35:1239–51.

Gozlan, R. E., J. R. Britton, I. Cowx, and G. H. Copp. 2010. Current knowledge on non-native freshwater fish introductions. Journal of Fish Biology 76:751–86.

Grossman, G. D., R. E. Ratajczak, C. M. Wagner, and J. T. Petty. 2010. Dynamics and regulation of the southern Brook Trout (*Salvelinus fontinalis*) population in an Appalachian stream. Freshwater Biology 55:1494–508.

Habera, J. W., M. A. Kulp, S. E. Moore, and T. B. Henry. 2010. Three-pass depletion sampling accuracy of two electric fields for estimating trout abundance in a low-conductivity stream with limited habitat complexity. North American Journal of Fisheries Management 30:757–66.

Habera, J. W., and S. E. Moore. 2005. Managing southern Appalachian Brook Trout: a position statement. Fisheries 30(7):10–20.

Habera, J. W., R. J. Strange, B. D. Carter, and S. E. Moore. 1996. Short-term mortality and injury of Rainbow Trout caused by three-pass AC electrofishing in a southern Appalachian stream. North American Journal of Fisheries Management 16:192–200.

Habera, J. W., R. J. Strange, and S. E. Moore. 1992. Stream morphology affects trout capture efficiency of an AC backpack electrofisher. Journal of the Tennessee Academy of Science 67:55–8.

Hitt, N. P., C. A. Frissell, C. C. Muhlfeld, and F. W. Allendorf. 2003. Spread of hybridization between native Westslope Cutthroat Trout, *Oncorhynchus clarki lewisi*, and nonnative Rainbow Trout, *Oncorhynchus mykiss*. Canadian Journal of Fisheries and Aquatic Sciences 60:1440–1451.

Hoxmeier, R. J. H., and D. J. Dieterman. 2016. Long-term population demographics of native Brook Trout following manipulative reduction of an invader. Biological Invasions 18:2911–2922.

Kanno, Y., K. C. Pregler, N. P. Hitt, B. H. Letcher, D. J. Hocking, and J. E. B. Wofford. 2016. Seasonal temperature and precipitation regulate Brook Trout young-of-the-year abundance and population dynamics. Freshwater Biology 61:88–99.

King, W. 1937. Notes on the distribution of native, speckled, and Rainbow Trout in the streams at Great Smoky Mountains National Park. Journal of the Tennessee Academy of Science 12:351–6.

King, W. 1938. A program for the management of fish resources in Great Smoky Mountains National Park. Transactions of the American Fisheries Society 68:86–95.

Kulp, M. A., and S. E. Moore. 2000. Multiple electrofishing removals for eliminating Rainbow Trout in a small southern Appalachian stream. North American Journal of Fisheries Management 20:259–66.

Kulp, M. A., and S. E. Moore. 2005. A case history in fishing regulations in Great Smoky Mountains National Park: 1934–2004. North American Journal of Fisheries Management 25:510–24.

Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic Rainbow Trout into stream populations of native Brook Trout in the southern Appalachian Mountains. Transactions of the American Fisheries Society 114:195–203.

Larson, G. L., S. E. Moore, and D. C. Lee. 1986. Angling and electrofishing for removing nonnative Rainbow Trout from a stream in a National Park. North American Journal of Fisheries Management 6:580–5.

Lennon, R. E., and P. D. Parker. 1959. Reclamation of Indian Creek and Abrams Creek in Great Smoky Mountains National Park. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 306.

Lindeman, A. A., J. W. A. Grant, and C. M. Desjardins. 2015. Density-dependent territory size and individual growth rate in juvenile Atlantic Salmon (*Salmo salar*). Ecology of Freshwater Fish 24:15–22.

Lobón-Cerviá, J. 2007. Density-dependent growth in stream-living Brown Trout *Salmo trutta* L. Functional Ecology 21:117–24.

Lobón-Cerviá, J. 2009. Why, when and how do fish populations decline, collapse and recover? The example of Brown Trout (*Salmo trutta*) in Rio Chaballos (northwestern Spain). Freshwater Biology 54:1149–1162.

McGrath, C. C., and W. M. Lewis Jr. 2007. Competition and predation as mechanisms for displacement of Greenback Cutthroat Trout by Brook Trout. Transactions of the American Fisheries Society 136:1381–92.

McHugh, P., and P. Budy. 2005. An experimental evaluation of competitive and thermal effects on Brown Trout (*Salmo trutta*) and Bonneville Cutthroat Trout (*Oncorhynchus clarkii utah*) performance along an altitudinal gradient. Canadian Journal of Fisheries and Aquatic Sciences 62:2784–2795.

Meyer, K. A., J. A. Lamansky Jr., and D. J. Schill. 2006. Evaluation of an unsuccessful Brook Trout electrofishing removal project in a small Rocky Mountain stream. North American Journal of Fisheries Management 26:849–60.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. Fisheries 14(6):22–38.

Milner, N. J., J. M. Elliott, J. D. Armstrong, R. Gardiner, J. S. Welton, and M. Ladler. 2003. The natural control of salmon and trout populations in streams. Fisheries Research 62:111–25.

Moore, S. E., M. A. Kulp, J. Hammonds, and B. Rosenlund. 2005. Restoration of Sams Creek and an assessment of Brook Trout restoration methods, Great Smoky Mountains National Park. National Park Service Technical Report NRTR-2005/342.

Moore, S. E., G. L. Larson, and B. Ridley. 1986. Population control of exotic Rainbow Trout in streams of a natural area park. Environmental Management 10:215–19.

Nakano, S., S. Kitano, K. Nakai, and K. D. Fausch. 1998. Competitive interactions for foraging microhabitat among introduced Brook Charr, *Salvelinus fontinalis*, and native Bull Charr, *S. confluentus*, and Westslope Cutthroat Trout, *Oncorhynchus clarki lewisi*, in a Montana stream. Environmental Biology of Fishes 52:345–55.

NPS (National Park Service). 2006. Management policies 2006. U.S. Government Printing Office. Washington, D.C.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of Brook Trout on native Cutthroat Trout. Ecological Applications 14:754–72.

Powers, E. B. 1929. Freshwater studies: I. The relative temperature, oxygen content, alkali reserve, the carbon dioxide tension and pH of the water of certain mountain streams at different altitudes in the Smoky Mountains National Park. Ecology 10:97–111.

R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Taniguchi, Y., F. J. Rahel, D. C. Novinger, and K. G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences 55:1894–901.

Thibault, I., and J. Dodson. 2013. Impacts of exotic Rainbow Trout on habitat use by native juvenile salmonid species at an early invasive stage. Transactions of the American Fisheries Society 142:1141–50.

Utz, R. M., and K. J. Hartman. 2009. Density-dependent individual growth and size dynamics of central Appalachian Brook Trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 66:1072–80.

Van Deventer, J. S., and W. S. Platts. 1989. Microcomputer software system for generating population estimates from electrofishing data: user's guide for Microfish 3.0. U.S. Forest Service General Technical Report INT-254.

Vinson, M. R., E. C. Dinger, and D. K. Vinson. 2010. Piscicides and invertebrates: after 70 years, does anyone really know? Fisheries 35:61–71.

West, J. L., S. E. Moore, and M. R. Turner. 1990. Evaluation of electrofishing as a management technique for restoring brook trout in Great Smoky Mountains National Park. National Park Service, Research/Resource Management Report SER-90/01, Atlanta.

Whiteley, A. R., S. W. Fitzpatrick, W. C. Funk, and D. A. Tallmon. 2015. Genetic rescue to the rescue. Trends in Ecology and Evolution 30:42–9.