Transactions of the American Fisheries Society 124:613–622, 1995
American Fisheries Society

Ebb and Flow of Encroachment by Nonnative Rainbow Trout in a Small Stream in the Southern Appalachian Mountains

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Abstract.—Brook trout *Salvelinus fontinalis* is the native salmonid species of streams in the southern Appalachian Mountains. The present distribution of this species, once widespread from headwaters to lower reaches of large streams, is restricted to mostly headwater areas. Changes in the distribution of native brook trout in the presence of nonnative rainbow trout *Oncorhynchus mykiss* have been documented in Great Smoky Mountains National Park. When rainbow trout were first found in a tributary (Rock Creek) in the park in 1979, a study was begun to assess changes through time in distribution and abundance of rainbow trout in Rock Creek and to compare the brook trout and rainbow trout associations in Rock Creek with associations found in other park streams. Abundance of brook trout was low in the downstream sections of Rock Creek in 1979–1993. Brook trout abundance was highest in the steep-gradient, pool-dominated headwater section which was only 2 km from the confluence of Rock Creek and Cosby Creek. Rainbow trout were present in low densities in Rock Creek during the same period. Although rainbow trout were most abundant in the lower stream sections and never found in the headwater section, adult and age-0 rainbow trout were found in the middle section in 1988. Rainbow trout were absent in the middle section in 1991, but one large adult rainbow trout was present in the section in 1992 and 1993. Floods, freshets, and periods of low stream discharge appeared to play an important role in the distribution and population structure of rainbow trout in Rock Creek. The lower portion of Rock Creek was poor trout habitat because the sections were dominated by cobble–rubble substrate and shallow riffle areas. Stream habitat appeared to be better suited for brook trout than for rainbow trout in the steep-gradient upstream sections which were dominated by boulder-cobble substrate and deep pools. The results of this study suggest that encroachment by rainbow trout can exhibit considerable ebb and flow in steep-gradient tributaries in the park, and they suggest substantial evolutionary adaptation by brook trout to the hydrological conditions in the Rock Creek drainage.

Nonnative salmonids have been introduced in many areas of the world without much apparent concern about their impact on native salmonid species (Fausch 1988). In many instances, native salmonids have been displaced or their population distribution has been reduced in the presence of introduced species (Fausch 1988, 1989). Although interspecific competitive interactions and interacting effects of temperature and stream channel gradient have been associated with losses of native salmonids, Fausch (1989) concluded that there were few consistent relationships among altitude, latitude, and temperature limits for habitat selection by brook trout *Salvelinus fontinalis* and other stream salmonids. This is not surprising, given the complex and diverse nature of migratory and residential behaviors of salmonid fishes (Northcote 1992). In this paper, we specifically explore temporal changes in the distribution of nonnative rainbow trout *Oncorhynchus mykiss* invading a stream inhabited by native brook trout.

The brook trout is the native salmonid species of streams in the southern Appalachian Mountains. However, the distribution of the species has been reduced mostly to small headwater areas since 1900 (Kelly et al. 1980). The decline of brook trout in the southern Appalachian Mountains is best documented in Great Smoky Mountains National Park (King 1937; Lennon 1967; Kelly et al. 1980). Before 1900, brook trout were found in streams throughout the park, with the exception of low-gradient streams less than 500 m in elevation (King 1937). Loss of brook trout in the lower reaches of streams between 1900 and the mid-1930s resulted from logging practices and overfishing (Moore et al. 1983). Although forests became reestablished within the watersheds of the park following the cessation of logging, and although fishing regulations were implemented to protect native fish, brook trout did not return to lower stream reaches. Instead, introduced nonnative rainbow trout thrived

in the lower reaches of the streams and eventually immigrated upstream into areas inhabited by brook trout. Larson and Moore (1985) described the encroachment process in streams of the park. First, a few adult rainbow trout invaded allopatric brook trout waters upstream. Recruitment of brook trout declined, followed by a decline in the number of adult brook trout as the number of rainbow trout increased. Eventually, when abundance of adult brook trout was low, rainbow trout recruitment increased. Indirect evidence of the competitive advantage of rainbow trout over brook trout was apparent in instances when rainbow trout were removed from sympatric assemblages of brook and rainbow trout, and abundance and biomass of brook trout populations rebounded (Moore et al. 1983).

This typical invasion of brook trout habitat by rainbow trout has not occurred in the Cosby Creek Drainage of Great Smoky Mountain National Park. Cosby Creek is atypical of most park streams because it does not have low-gradient, coldwater sections (S.E.M., unpublished data). The main portion of Cosby Creek is considered poor trout habitat because it is warm and dominated by shallow riffle areas (S.E.M., unpublished data). Rainbow trout have inhabited the main stem of Cosby Creek for decades (Kelly et al. 1980), but they were not found in the headwaters of the main stream or in its tributaries during stream surveys conducted between 1936 and 1975 (King 1937; Lennon 1967; Kelly et al. 1980). In 1979, a sympatric assemblage of rainbow trout, brook trout, and two nongame fish species was discovered in the first 100 m of Rock Creek upstream from its confluence with Cosby Creek. This discovery prompted us to begin a long-term study, conducted intermittently from October 1979 through July 1993, to determine if rainbow trout would continue to invade upstream reaches. Objectives of the study were to document changes in the distribution and abundance of rainbow trout through time and to compare brook trout and rainbow trout associations in Rock Creek with associations found in other park streams.

Study Area

The confluence of Rock Creek with Cosby Creek is at low elevation (625 m), and the headwaters of Rock Creek extend to about 1,300 m (Figure 1). A road parallels the lower portion of Cosby Creek and crosses Rock Creek about 30 m upstream from the confluence of the two streams. The lower portion of the Rock Creek watershed is second-growth forest; the upper portion is predominantly old-growth forest. Cosby Creek is open to fishing for rainbow trout, with the condition that any captured native brook trout be released. Rock Creek has been closed to fishing since 1976.

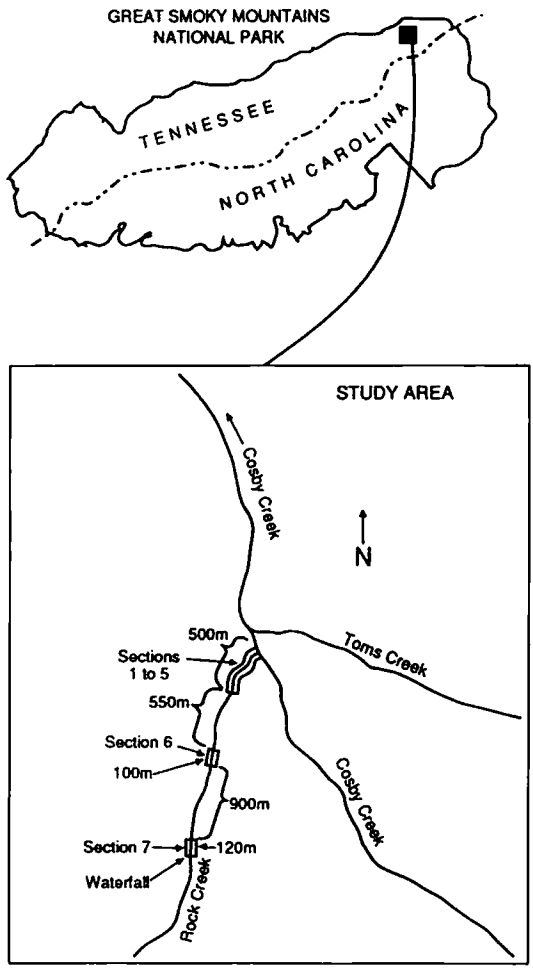

FIGURE 1.—Location of the study area and the sampling sections in Great Smoky Mountains National Park.

For sampling purposes, Rock Creek was divided into seven sequentially numbered sections starting with section 1 at the confluence of Rock Creek and Cosby Creek and proceeding upstream (Table 1). Each section was 100 m long except for section 7, which was 120 m long (Figure 1). The upper end of section 7 was at the base of a waterfall 1.5 m high. The first five sections were contiguous so that changes in the distribution of rainbow trout could be assessed during the early stages of encroachment. The beginning of section 6 was 550 m upstream from the end of section 5, and the beginning of section 7 was 900 m upstream from

TABLE 1.—Stream channel characteristics of study sections of Rock Creek, May 1980.

Section	Mean width (m)	Minimum elevation (m)	Mean gradient (%)	Number of pools deeper than 0.5 m	Number of pools per 100 m^2	Dominant substrate types	Shallow riffle area (%)
1	3.83	625	5.5	4	1.04	Cobble-rubble	47.5
2	5.03	631	6.5	9	1.79	Cobble-rubble	60.0
3	4.34	640	7.3	5	1.15	Cobble-rubble	60.0
4	5.77	651	7.5	11	1.91	Boulder-cobble-rubble	36.3
5	5.06	663	8.3	11	2.17	Boulder-cobble	12.5
6	4.71	738	10.3	16	3.40	Boulder-cobble	7.5
7	3.28	854	11.5	19	4.82	Boulder-cobble	1.3

the end of section 6. Elevation and gradient of the stream increased from section 1 to section 7 (Table 1). The streambed was dominated by cobble and rubble in the lower sections and by boulder and cobble in sections 5, 6, and 7. Pool density increased with increased channel gradient upstream, whereas the amount of shallow riffle area decreased (Table 1).

Methods

Long-term changes in the discharge of Rock Creek were estimated from discharge measurements of Cosby Creek recorded at a gauging station located near the park boundary from January 1977 through December 1988 (USGS 1966–1982; Lowery et al. 1983–1989). From January 1989 through December 1992, discharge of Cosby Creek was estimated from data collected at a gauging station on Little River (5th order) on the north-central edge of the park near the park boundary about 30 km west from Cosby Creek (Lowery et al. 1990; Flohr et al. 1991, 1993; Mercer et al. 1992). Discharge data for Little River were not available for 1993. A significant linear relationship was found between the mean daily discharge per month of Cosby Creek and Little River for water-years 1984 through 1987 (Discharge of Cosby Creek = $1.246 + 0.090x$; $P < 0.001$; $r^2 = 0.867$). The calculated mean daily discharge per month, however, did not adequately characterize any localized torrential flows between 1989 and 1992 in Cosby Creek. A limited number of discharge measurements of Rock Creek were made with a Marsh McBirney (model 201D) portable flowmeter near the confluence of Cosby Creek.

TABLE 2.—Rock Creek study sections sampled (×) in 1979–1993.

Year	Sample period	Section 1	2	3	4	5	6	7
1979	Oct	×						×
1980	May	×	×	×	×	×	×	×
1980	Sep–Oct	×	×	×	×	×	×	×
1981	Sep–Oct		×	×	×	×	×	×
1988	Jul	×	×	×	×		×	×
1991	Jun–Jul[a]	×					×	×
1992	Jun	×					×	×
1993	Jun–Jul	×		×		×	×	×

[a] Before a major flood (expected return interval, >100 years).

We sampled Rock Creek periodically to determine species composition and abundance of fish communities (Table 2). During each sampling trip, fish were collected by electrofishing (three passes per section) with block nets set up downstream, as described by Moore et al. (1983). Captured fish were placed in buckets and later measured and weighed (Moore et al. 1983). After it was processed, each trout was returned to its capture location. To facilitate the return of trout to their original locations, we used large stones to mark capture locations of large trout and smaller stones for smaller trout. We tried to return nontrout to their points of capture also. Sums of the fish collected from three passes per section on each sampling date provided measures of relative abundances of trout and nontrout. The fish community in a section of Cosby Creek was sampled in May 1980. The sample reach extended 50 m upstream and 50 m downstream from the confluence of Rock Creek and Cosby Creek.

In conjunction with the sampling of fish communities, habitat variables also were measured. We determined stream width by measuring each section at intervals of 5 m with a measuring tape. Sample area was calculated as average width times the length of each section. The areas calculated for the May 1980 sample were used to estimate fish density per section for all years. Composition of the stream bottom was estimated by eye for each section (Table 1). Pool depths were estimated by eye. Elevation was determined with an altimeter, and gradient was determined with a clinometer.

TABLE 3.—Mean minimum–maximum daily discharges (m^3/s) of Cosby Creek, January–December, in various years from 1977 to 1992.

Years	Jan–Mar	Apr–Jun	Jul–Sep	Oct–Dec
1977–1984	0.67–1.44	0.64–1.39	0.32–0.84	0.32–0.85
1985–1988	0.47–1.15	0.28–0.80	0.19–0.57	0.15–0.54
1989–1992[a]	1.22–1.65	0.66–1.04	0.33–0.87	0.42–1.49
1977–1992	0.76–1.33	0.55–1.16	0.29–0.78	0.30–0.93

[a] Estimated from Little River.

Regression analyses and *t*-tests were performed with SYSTAT (Wilkinson 1987). We calculated average yearly stream discharge for Cosby Creek by averaging the flows for each month. An analysis of variance (ANOVA) was used to test for differences in discharge between years, and Fisher's protected least-significant-difference test was used to conduct multiple comparisons between three year-groups: 1977–1984, 1985–1988, and 1989–1992. A Bonferroni adjustment ($P \leq 0.02$) to the *P*-value was made to account for making multiple comparisons (Johnson and Wichern 1982).

Results

Discharge of Cosby Creek and Rock Creek

Mean daily discharge of Cosby Creek typically varied between 0.55 and 1.33 m^3/s in winter and spring and between 0.29 and 0.93 m^3/s in summer and early fall (Table 3). As exceptions, mean monthly discharges from 1985 through 1988 (0.50 m^3/s) were significantly lower than those between 1977 and 1984 (0.77 m^3/s, $P < 0.02$) and 1989 to 1992 (0.93 m^3/s, $P < 0.02$). Although ongoing measurements of Rock Creek discharge were not made, measurements in July and August 1991 indicated that discharge of Rock Creek was 12–20% of the discharge of Cosby Creek. However, in July 1991, a large flood (exceeding a 100-year recurrence interval) occurred in the Rock Creek drainage (J. Lewis, U.S. Geological Survey, personal communication). Flash floods of varying intensities (7–15 m^3/s) occurred in Cosby Creek infrequently, but at any time of year, from localized torrential rainfalls, although none occurred from April 1985 to December 1988 (data not shown).

Species Composition and Abundance in Rock Creek

Six fish species were collected in Rock Creek: brook trout, rainbow trout, longnose dace *Rhinichthys cataractae*, blacknose dace *R. atratulus*, mottled sculpin *Cottus bairdi*, and central stoneroller *Campostoma anomalum*. Only one central stoneroller was collected, and this species was not included in data analyses. Nontrout fishes were most abundant in sections 1–4, and none were found in section 7 (Figure 2).

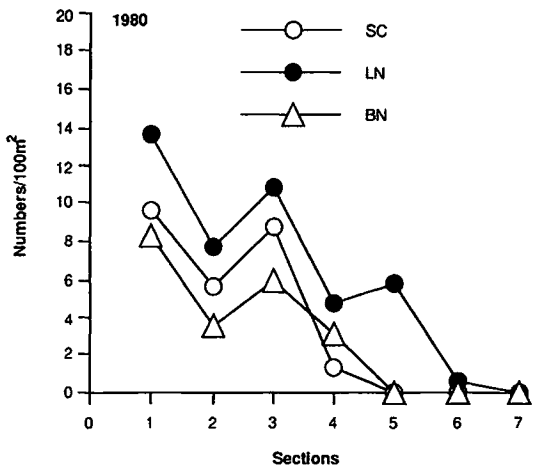

FIGURE 2.—Abundances of mottled sculpin (SC), longnose dace (LN), and blacknose dace (BN) by section in Rock Creek, September–October 1980.

Brook trout were present in each section of Rock Creek sampled on each sampling date. It was the only fish species present in section 7. Abundance of adult brook trout always was highest in section 7 and decreased downstream (Figure 3). Abundance of age-0 brook trout was variable but generally increased from section 1 to section 7 except in 1981, when age-0 fish were most abundant in sections 4–6 (Figure 4). Abundance of age-0 brook trout was high in 1993.

Adult rainbow trout abundance was low each year, but was typically higher in sections 1–3 than in sections 4–6 (Figure 3). Rainbow trout were present in sections 1–3 in May 1980 and in sections 1–3 and 5 (1 fish) during September–October 1980. In 1981, they were present in sections 2–4 (section 1 was not sampled). In 1988, rainbow trout were at the maximum abundance observed during this study, and they were present in sections 1–6. In 1991, rainbow trout were present in section 1 (sections 2–5 were not sampled) but not in section 6, whereas they were present in sections 1 and 6 (1 fish) in 1992 (sections 2–5 were not sampled) and in sections 1, 3, 5, and 6 (1 fish) in 1993 (sections 2 and 4 were not sampled).

Abundance of age-0 rainbow trout was low on all sampling dates (Figure 4). Age-0 fish typically were present in sections 1 and 2 except in 1988, when they were present in sections 1–6. No age-0 fish were captured in May 1980.

Mean weight of rainbow trout in section 6 in

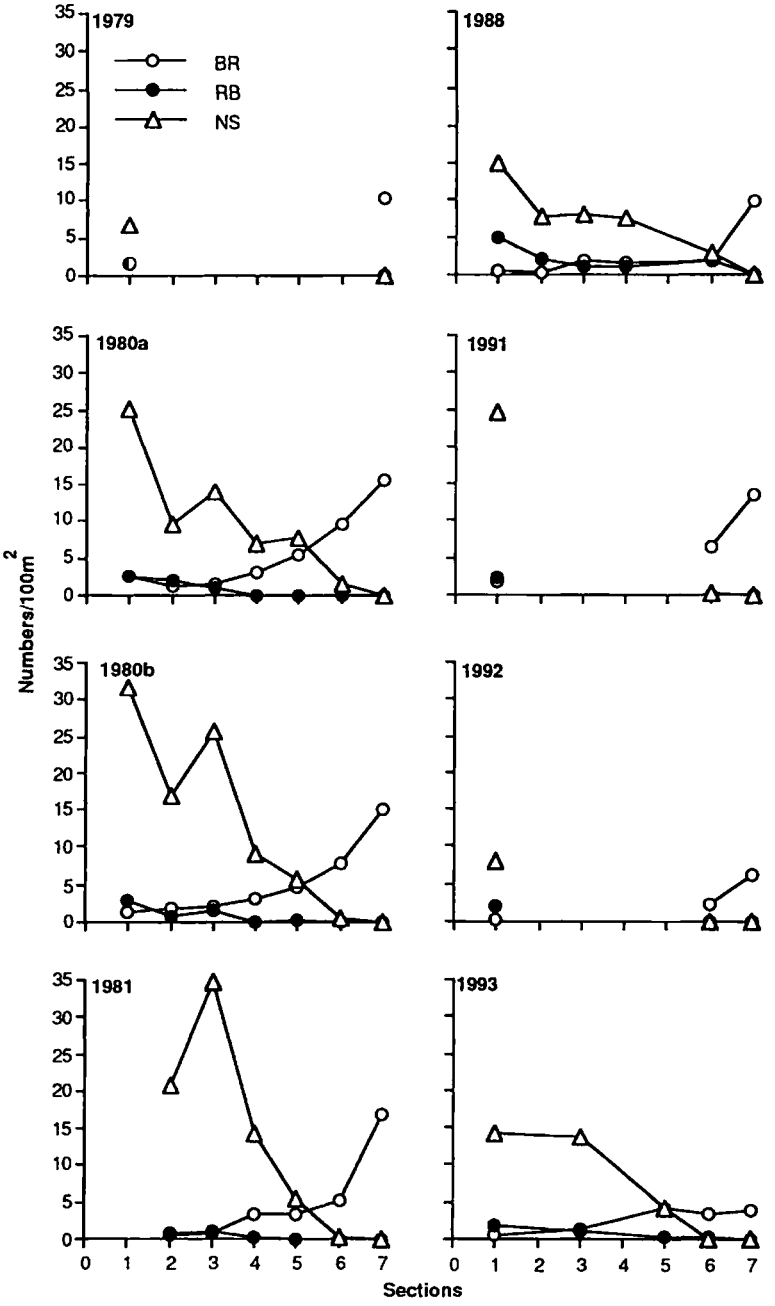

FIGURE 3.—Abundances of adult brook trout (BR), adult rainbow trout (RB), and nonsalmonid fishes (NS) by section in Rock Creek during various years from 1979 to 1993 (1980a sampling occurred in May, 1980b sampling in September–October).

1988 was not significantly greater (t-test, $P = 0.10$) than weights in sections 1–4 (section 5 was not sampled). In 1992 and 1993, however, rainbow trout in section 6 had mean body weights that were in the 98th (1992) and 99.9th (1993) percentiles of the weight distributions of fishes in downstream sections (L. Ganio, Oregon State University, personal communication; Table 4).

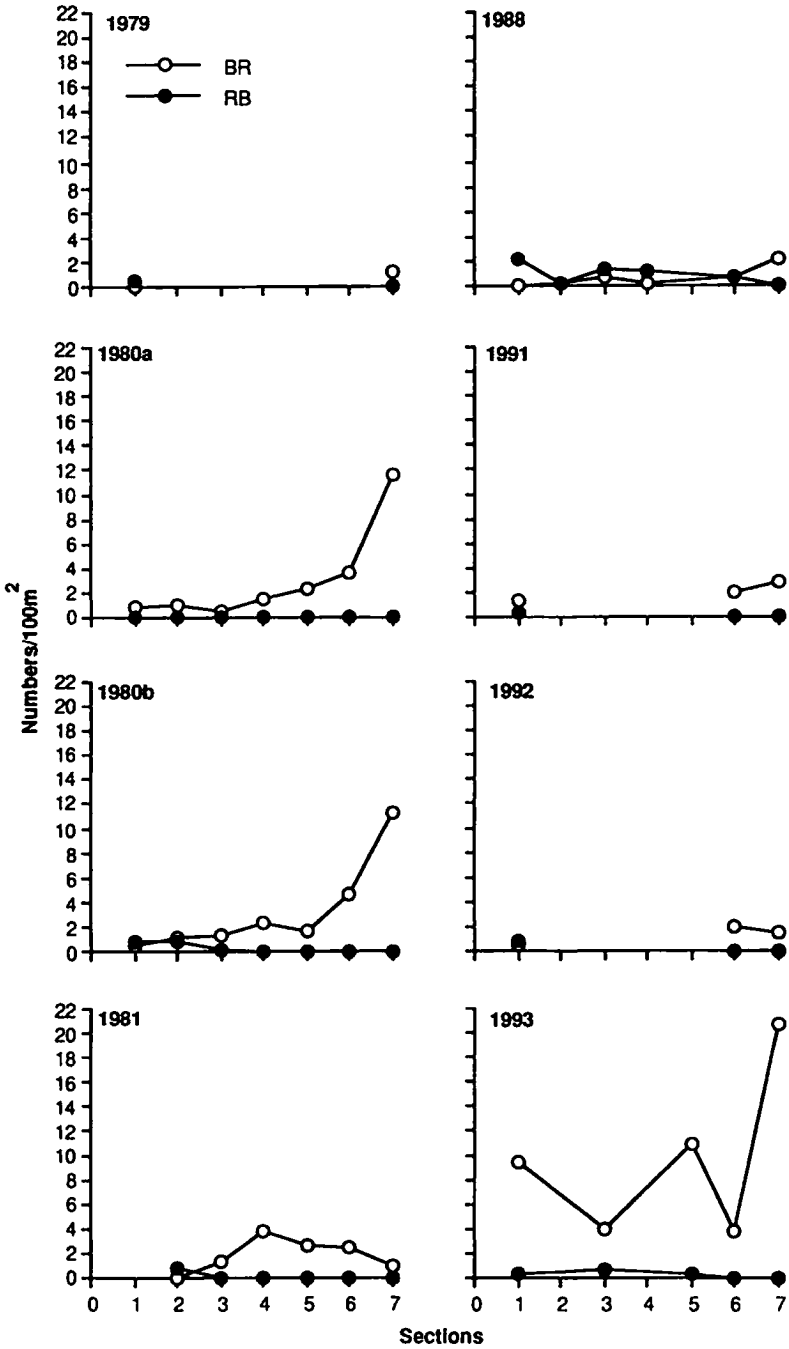

FIGURE 4.—Abundances of age-0 brook trout (BR) and rainbow trout (RB) by section in Rock Creek during various years from 1979 to 1993 (1980a sampling occurred in May, 1980b sampling in September–October).

Species Composition and Abundance in Cosby Creek

Brook trout, rainbow trout, longnose dace, blacknose dace, and mottled sculpin were present in Cosby Creek in May 1980 (Table 5). Age-0 and adult brook trout were less abundant in Cosby Creek than they were in section 1 of Rock Creek (Figures 3, 4), whereas abundance of adult rainbow

TABLE 4.—Average body weights (g) of adult rainbow trout in the seven study sections of Rock Creek, 1979–1993.

Year	Section 1	2–4	5	6	7
1979	40.0				0
1980[a]	47.8		0	0	0
1980[b]	42.8	38.0	56.0	0	0
1981		59.0–62.8	0	0	0
1988	39.6	29.8–48.9		39.8	0
1991	53.9			0	0
1992	94.3			170.0[c]	0
1993	81.9	46.1	79.5	184.0[c]	0

[a] May sample.
[b] Sep–Oct sample.
[c] One fish.

TABLE 5.—Abundance of brook trout, rainbow trout, and nontrout species in Cosby Creek at the confluence with Rock Creek, May 1980.

Species, life stage	Number/100 m^2
Brook trout	
Adult	1
Age-0	0
Rainbow trout	
Adult	4
Age-0	0.8[a]
Longnose dace	4
Blacknose dace	3
Mottled sculpin	6

[a] Presumably, most had not emerged from the gravel bed.

trout was similar. Abundance of age-0 rainbow trout was low in Cosby Creek.

Discussion

This study documented differences in the distributions of native brook trout and nonnative rainbow trout in different sections of Rock Creek relative to differences in habitat in those stream sections (sensu Moyle and Vondracek 1985). The high abundances of mottled sculpin, longnose dace, and blacknose dace and the low abundances of brook trout and rainbow trout in sections 1–4 suggests that these sections were more optimal for the nontrout species than for the two salmonid species (Hynes 1970; Becker 1983; Facey and Grossman 1992). In contrast, the middle (section 6) and uppermost (section 7) stream sections appeared to be better habitat for brook trout than for the nontrout species and rainbow trout. These results suggested that the habitat in the 2,170-m-long study area shifted quickly, and that the fish community changed with the habitat. Similar trends have been observed elsewhere in mountain streams, but usually gradients occurred over much longer distances (Burton and Odum 1945; Sheldon 1968; Gard and Flittner 1974).

This study also documented that nonnative rainbow trout were present in Rock Creek from 1979 to 1993 and that the brook trout–rainbow trout associations in Rock Creek were different from those observed by others (Larson and Moore 1985; Larson et al. 1986) in other park streams (Table 6). First, the elevation of Rock Creek at its confluence with Cosby Creek is more than 300 m lower than other low-elevation sections of streams in which brook and rainbow trout coexist. This is important because the streams at higher elevation, especially the low-gradient sections, are colder in summer than the low-gradient sections of Rock Creek (Silsbee and Larson 1982). Second, the density of rainbow trout in the main stems was much greater than in Cosby Creek, which provides greater potential for adult rainbow trout to invade the tributaries. Third, the density of rainbow trout was much higher in the lower sections of the tributaries at high elevation, providing greater potential for adult rainbow trout to reproduce and encroach upon the brook trout waters upstream. Fourth, the

TABLE 6.—Comparison of selected habitat variables of Rock Creek with those of other park streams inhabited by brook trout and rainbow trout.

Variable[a]	Rock Creek (1979–1991)[b]	Other park streams[c]
Elevation (m) of tributary at confluence of main stream	625	≥920
Channel gradient of tributary near confluence of main stream	Low	Low–moderate
Density of adult rainbow trout in main stream	4[d]	14–17
Density of adult rainbow trout in tributary near confluence	<1–5	10–12
Density of sympatric adult brook trout in tributary near confluence of main stream	1–3	0–1
Density of allopatric adult brook trout in upper tributary section	9–17	12–18
Density of age-0 rainbow trout in tributary near confluence of main stream	0–2	5–7
Density of sympatric age-0 brook trout in tributary near confluence of main stream	0–2	0–1
Density of age-0 brook trout in upper tributary sections	3–13	7–14

[a] Density values are for 100 m^2 of streambed.
[b] Before the flood in 1991.
[c] From Larson and Moore (1985) and Larson et al. (1986).
[d] Cosby Creek.

densities of age-0 rainbow trout were much higher in the lower sections of high-elevation tributaries than in Rock Creek. However, in section 7, which contained only brook trout, densities of adult and age-0 fish were similar to those in higher elevation streams in the park. Based on these results, it seems that the lower sections of Rock Creek are poor habitat for rainbow and brook trout, whereas the headwater section is good habitat for brook trout.

Rainbow trout entered section 6 of Rock Creek and reproduced between 1981 and 1988. Studies of other park streams (Larson and Moore 1985) suggest the encroachment process during this period was at an intermediate stage because adult and age-0 brook trout were still present in section 6 in 1988. Shortly thereafter, encroachment seemed to have reversed, because only brook trout were found in section 6 in 1991. We believe the invasion of upstream areas by rainbow trout between 1981 and 1988 may have been associated with changes in the discharge of Rock Creek. As noted earlier, the discharge of Cosby Creek (and presumably Rock Creek) was low in 1985–1988. This period of reduced discharge in Rock Creek was presumably associated with increased water temperatures in spring, summer, and fall. Although we lack data from Rock Creek to support this conclusion, limited water temperature data from another park stream (Little River) was inversely related to discharge in July and August (regression analysis, $P = 0.01$, $r^2 = 0.342$; USGS 1967–1977, 1979–1982). Increased water temperatures in 1985–1988 in the upstream sections of Rock Creek would have benefitted rainbow trout because the optimal temperature for this species appears to be higher than that for brook trout (McCauley and Pond 1971; McCormick et al. 1972; Peterson et al. 1979; Power 1980). The lack of freshets between 1985 and 1988 could have enhanced the successful encroachment of adult rainbow trout and survival of embryos and age-0 rainbow trout (Seegrist and Gard 1972). If reduced discharge and absence of freshets in Rock Creek favored rainbow trout encroachment and reproduction in upstream sections of the creek between 1985 and 1988, the return of normal discharge patterns (including freshets) between 1989 and 1991 (before the exceptionally large flood) could have reversed the encroachment process and again favored brook trout. During periods of normal and higher stream discharge, rainbow trout did not appear to be as well adapted as brook trout to the steep stair-stepped portions of Rock Creek.

Brook trout prefer low-gradient, coldwater streams (Platts 1976; Power 1980) but also appear to be well adapted to the steep, stair-stepped sections of streams in Great Smoky Mountains National Park. This conclusion is supported by the following data: (1) brook trout have been in the park area for 2.5 to 3 million years (David Etnier, University of Tennessee, personal communication); (2) brook trout densities are highest in pools, those portions of the stair-stepped streams with low gradient and reduced turbulence (Cunjak and Green 1984; Larson and Moore 1985); (3) body size of adult brook trout is small (Larson and Moore 1985); (4) adult brook trout exhibit limited dispersal from their "home" sections in steep stair-stepped streams in the park (Moore et al. 1985); and (5) individual female brook trout have a low fecundity (Lennon 1967). These traits suggest that brook trout in the steep stair-stepped sections of the park streams increase their potential for survival by reducing the amount of dispersal; maintaining their highest densities in the low gradient and turbulent portions of the stream (pools), which probably reduces their exposure to changes in stream flow; maintaining a high population density, which reduces the importance of each individual to the perpetuation of the population; increasing the number of potential spawners; and retaining small size, which makes more hiding sites available to them during floods and freshets.

The presence of a few large rainbow trout upstream of the main rainbow trout population was typical of observations made elsewhere in the park (Larson and Moore 1985) and suggests that this species relies on large fish to invade park streams. This conclusion supports the observations by Harvey and Stewart (1991), who showed that the largest individuals of several fish species were the first to colonize newly created pools in small streams in eastern Tennessee. The observation that average size of reproducing rainbow trout in section 6 in 1988 was smaller than the single rainbow trout in 1992 and 1993 also was typical of observations made elsewhere in the park (Larson and Moore 1985). The mean body weight per fish in reproducing populations of rainbow trout is reduced because the population is usually dominated by several age-classes of smaller fish.

Rainbow trout were not present in Rock Creek in 1975 (Kelly et al. 1980), but were present in the lower section in 1979. The presence of rainbow trout in the creek between 1979 and 1993 may be related to the 1976 closure of the creek to fishing. Even limited fishing pressure in habitats like the

lower portions of Rock Creek could seriously impact the abundance of rainbow trout because the species' density is low. Removal of any rainbow trout from these sections could have a serious impact on rainbow trout reproduction, which was low in all years of this study.

In summary, it appears that there is considerable ebb and flow in the distribution of rainbow trout in Rock Creek. Indeed, rainbow trout may have an ephemeral existence in the stream. Although the results also suggest that the lower portion of Rock Creek is poor trout habitat, habitat quality quickly improves upstream. Normal flow conditions are apparently more favorable for native brook trout than for rainbow trout. However, habitat quality may improve upstream for rainbow trout in the future if changes in global climate (Schneider 1989) result in extended periods of reduced flows in the steep-gradient sections of Rock Creek and, perhaps, of tributaries parkwide. Nonetheless, fishery managers in the southern Appalachian Mountains should not view the results of this study as the typical invasion scenario for rainbow trout. Unlike the situation at Rock Creek, densities of rainbow trout in the lower sections of other mountain streams are quite high, and invasion by these nonnative salmonids into headwater sections undoubtedly will continue under suitable conditions. Encroachment by nonnative salmonids has great potential to eliminate remnant populations of native brook trout, which are important sources of genetic diversity (Scudder 1989). Nonnative salmonids should be removed from selected mountain streams to ensure that management of brook trout remains a viable option. A major management objective should be to return native brook trout populations to their original distributions within selected watersheds. This is especially important for the numerous high-order and low-gradient mountain streams that are no longer inhabited by native brook trout.

Acknowledgments

We thank Wayne Singleton, Dave Mathews, Terresa Beam, Bob Dellinger, and Tim Broadbent for assistance in the field. Our thanks are extended to the members of the Uplands Field Research Laboratory and to M. D. Beal, S. Coleman, R. Herrmann, J. Gogue, and R. Pope for their support of the project. We particularly appreciated the constructive comments by three anonymous reviewers and Robert Gresswell. Lisa Ganio assisted with statistical analyses of the data. Ruth Jacobs edited the manuscript.

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Received April 29, 1994
Accepted January 15, 1995