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A Regional View of the Margin: Salmonid Abundance and Distribution in the Southern Appalachian Mountains of North Carolina and Virginia

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Abstract.—In the southern Appalachian Mountains, native brook trout *Salvelinus fontinalis* and introduced rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* are at the southern extremes of their distributions, an often overlooked kind of marginal habitat. At a regional scale composed of the states of Virginia and North Carolina, species were found to be distributed along latitudinal and elevational gradients. Native brook trout remain most common and abundant, decreasing both from north to south and from high to low elevations. Sympatry increases to the south, where rainbow and brown trout become more successful. For the region as a whole and within major drainages, allopatric and sympatric brook trout were generally found at higher elevations and rainbow and brown trout at lower elevations. Among drainages, elevations at which allopatric brook trout and rainbow trout are found generally increased to the south. A measure of effective elevation, which adjusts elevation for latitude, most clearly separated allopatric and sympatric brook trout from allopatric rainbow and brown trout.

In the southern Appalachian Mountains, salmonids are at the southern margin of their distributions in eastern North America. The original distribution of brook trout *Salvelinus fontinalis,* the only native salmonid, extended down the spine of the Appalachian Mountains through western Virginia and North Carolina and eastern Tennessee to northeastern Georgia (MacCrimmon and Campbell 1969). Stockings have not notably extended the distribution of brook trout in the southern Appalachians. Rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* were introduced into the region in the late 19th and early 20th centuries. In this paper I will refer to the three species collectively as "trout."

In the Great Smoky Mountains of North Carolina and Tennessee, introduced rainbow trout have generally been successful at lower elevations, and between the 1930s and the 1970s, brook trout have been increasingly restricted to upper headwater reaches (Kelly et al. 1980; Larson and Moore 1985). In Tennessee streams north of Great Smoky Mountains National Park, similar reductions in brook trout distribution during the 1970s have been reported (Bivens et al. 1985). Evidence of similar changes in other areas of the southern Appalachians is anecdotal. Brook trout now occur at the highest elevations, and rainbow and brown trout at lower elevations; up to several kilometers of sympatric coexistence occur between the allopatric sections (Bivens et al. 1985; Larson and Moore 1985). However, studies have been conducted on a limited geographic area in and near the Great Smoky Mountains National Park of North Carolina and Tennessee (e.g., Moore et al. 1983, 1986; Bivens et al. 1985; Larson and Moore 1985) and were not designed to consider patterns over the full range of latitudinal and elevational gradients in the region. Yet, the southern Appalachian region, from northern Virginia to northern Georgia, extends 700 km over 5° of latitude and includes thousands of kilometers of trout stream (Flebbe et al. 1988). Other studies have shown brook trout to be widely distributed and abundant in the Shenandoah National Park of Virginia (500 km north of Great Smoky Mountains National Park), where rainbow trout are rare and of limited distribution (Lennon 1961).

Latitude and elevation are two large-scale geographic factors that can influence trout abundance and distribution patterns, primarily through their influence on stream temperature, which increases with decreasing latitude and elevation. Stream temperature is a basic factor limiting the distribution of poikilothermic species like trout (Brett 1956; Krebs 1972). Temperature regimes governed by latitude and elevation interact with a species' temperature requirements to form a template of suitable thermal habitats on the regional landscape. Temperature requirements for individual species may be quite complex and depend on season, life stage, acclimation, fish condition, and

interactions with numerous other factors (Brett 1956; Power 1980). Nevertheless, in general terms, brook trout are slightly less tolerant of warm temperatures than are rainbow or brown trout (Needham 1969; Brett 1979; Peterson et al. 1979; Raleigh 1982; Raleigh et al. 1984, 1986) and are generally considered to be restricted to areas where mean July temperature does not exceed 21°C (MacCrimmon and Campbell 1969). Recent concerns about global warming have prompted consideration of possible restrictions in geographic distribution of salmonid species, especially brook trout, in the southern Appalachians (Meisner 1990). Although Meisner (1990) related large-scale patterns of brook trout distribution to elevation or latitude, he did not consider interactions with other salmonid species.

Elevation may also influence trout distributions secondarily through human activities that vary with elevation. In the southern Appalachian Mountains, the lower elevations were generally more accessible for removal of forest cover and for European settlement (Pyle 1985; Williams 1989). Land use changes and forest harvest practices often increase stream temperatures above those normal for the latitude and elevation by removing streamside vegetation (Brown and Krygier 1970; Swift and Messer 1971). Other stream habitat changes may follow land use changes. At lower elevations, streams may also be more accessible for angling and trout stocking programs.

This study is an analysis of extensive inventory data previously collected by state agencies. The southern Appalachian Mountain region properly includes mountain areas of Virginia, North Carolina, Tennessee, South Carolina, and Georgia. Due to the limited availability of suitable data, the region hereinafter is defined as the two-state coldwater region of North Carolina and Virginia. My objectives were to (1) determine abundance (i.e., occurrence and density) of the three salmonid species, collectively and individually, in sympatric and allopatric situations for the region as a whole; (2) determine the distribution of the three salmonid species across large-scale gradients of elevation and latitude for the region as a whole; and (3) determine abundance and distribution of the three salmonid species among and within major drainage basins of the region.

Methods

I analyzed existing inventories of coldwater streams conducted by the North Carolina Wildlife Resources Commission (Bonner 1983) and the Virginia Department of Game and Inland Fisheries (Mohn and Bugas 1980). These two states contain most of the trout streams in the southern Appalachians (Flebbe et al. 1988). From northeast to southwest, the area sampled extended nearly 700 km over more than 4° of latitude, from approximately 35°N to about 39°22′30″N. Both state agencies selected representative reaches of public waters, particularly those in the National Forests. North Carolina did not inventory streams in the Great Smoky Mountains National Park. The Virginia survey was designed to sample all potential trout streams in selected counties (Mohn and Bugas 1980), and the North Carolina survey was designed to sample previously identified trout streams (J. Borawa, North Carolina Wildlife Resources Commission, personal communication). Altogether, 979 trout streams, defined here as streams that actually had trout when sampled, were surveyed (471 North Carolina streams sampled 1978–1981; 508 Virginia streams sampled 1975–1979), mostly (95%) between May and October. Most sampled trout streams (87%) were first through third order. There were more fourth- and higher-order streams in North Carolina than in Virginia (20% versus 8%) and more second-order streams in Virginia than in North Carolina (50% versus 32%). First-order streams (13% in Virginia, 12% in North Carolina) and third-order streams (30% in Virginia, 35% in North Carolina) were of similar importance in the two states.

Most of the trout streams in Virginia (92%) were designated wild trout streams (not stocked), and 94% of the trout sampled in North Carolina streams were wild. Stocking history in the two states is largely undocumented, but all three salmonid species were probably extensively stocked in all accessible streams (Borawa, personal communication; L. Mohn, Virginia Department of Game and Inland Fisheries, personal communication). I assumed that all streams accessible for inventory were accessible for stocking of all three species in the past; however, the inventories were conducted to avoid sampling recently stocked fish (Bonner 1983; Mohn, personal communication).

In both states, each trout stream was sampled by single-pass electrofishing of a stream segment, generally 60–150 m long, to determine presence of salmonids (Mohn and Bugas 1980; Bonner 1983). I considered these to be samples of stream segments in the region rather than representative samples of particular streams because each stream was sampled only once and trout density in a given stream varies over time. Both states reported

trout density (number of individuals/m^2); however, these samples were not truly quantitative because multiple-pass depletion estimates (Zippin 1958) were not made. Therefore, I emphasized salmonid presence or absence in each stream sample. I did not adjust trout density estimates to account for fish missed by single-pass sampling because efficiency of electrofishing can be highly variable, depending on equipment used, skills of users, species of fish, size of fish, and stream environmental conditions (Bohlin et al. 1989). Instead, I assumed that trout densities were all underestimated by an unknown, random amount and used densities as relative estimates for comparisons within the region. Although I refer to these estimates as densities, they should be considered density indicators rather than true values. The nonparametric Kruskal–Wallis test was used for comparison of trout densities, followed by a nonparametric pairwise comparison procedure (Neter et al. 1990:646). Frequency distributions for density were log-normally distributed; therefore, geometric mean densities are reported.

Regional distribution patterns were analyzed with respect to gradients of latitude and elevation. In both inventories, elevation of the sample was given, and I estimated latitude from 7.5-minute U.S. Geological Survey (USGS) quadrangle sheets. To determine the combined effects of latitude and elevation, I constructed a model based on the general ecological rule that 100 miles of latitude is approximately equal to 1,000 ft of elevation (i.e., 1° of latitude is approximately equal to 200 m of elevation) in terms of climate gradients (Colinvaux 1986). I calculated effective elevation (m) for each sample point as

$$\text{Elev}_{\text{eff}} = \text{Elev} + 200(\text{Lat} - 35.0); \quad (1)$$

Elev and Lat are elevation (m) and latitude (°N), respectively. Effective elevation adjusts elevation for the climatic effect of latitude and is the elevation at 35°N that corresponds to the observed elevation and latitude for each sample location.

Each trout stream was assigned to one of seven stream classes based on presence of one or more trout species: allopatric brook, rainbow, or brown trout; sympatric brook and rainbow trout; sympatric brook and brown trout; sympatric brook, rainbow, and brown trout; and sympatric rainbow and brown trout. I compared (analysis of variance) average latitude, elevation, and effective elevation among these seven stream classes to test whether brook trout were at higher latitudes and elevations than rainbow and brown trout and whether sympatric streams were intermediate between allopatric streams.

Drainage basins are natural partitions of large geographic areas that can be used to reduce overall variability and summarize abundance and distribution patterns (Flebbe et al. 1988; Joyce et al. 1990). I subdivided the study region into eight major drainages based on USGS hydrologic units (Figure 1): Shenandoah River, James and Rappahannock Rivers, Roanoke River, New River, Tennessee River, Yadkin River, Catawba River, and Savannah River. The Tennessee River drainage includes parts of both North Carolina and Virginia, but most of the trout streams in these two states were in the high-elevation portions of southwestern North Carolina. The Savannah River drainage includes a few high-elevation headwater streams.

I used the SAS statistical package for personal computers for all analyses (SAS Institute 1985)—in particular, the generalized linear model procedure for analysis of variance (ANOVA)—and set significance levels at 0.05 for all tests.

Results

Regional Abundance

Total trout density in trout streams averaged 0.028/m^2, ranging from 0.0003/m^2 to 0.922/m^2. Overall, brook trout was the most prevalent species, occurring in 528 of the trout streams (54%), followed by rainbow trout (443 stream, 45%) and brown trout (276 streams, 28%).

Allopatric brook trout streams were the most common and contained the highest trout densities (Table 1). Brook trout densities declined from 0.044/m^2 in allopatry to 0.011, 0.010, 0.008/m^2 in sympatry with rainbow trout (68 streams), brown trout (51 streams), and both species (17 streams), respectively. Allopatric rainbow trout streams were also relatively common, and densities declined slightly (from 0.025/m^2) when rainbow trout were sympatric with brook trout (0.013/m^2), brown trout (0.014/m^2, 116 streams), or both (0.007/m^2) trout species. Rainbow trout densities were not significantly different from brook trout densities in sympatric streams (Wilcoxon signed-rank test; $P > 0.50$). Brown trout streams were less common and densities of this species were generally low regardless of sympatry with other salmonids (0.005–0.007/m^2).

Regional Distribution

Streams with the highest species-specific trout densities (top 25% of densities for each species)

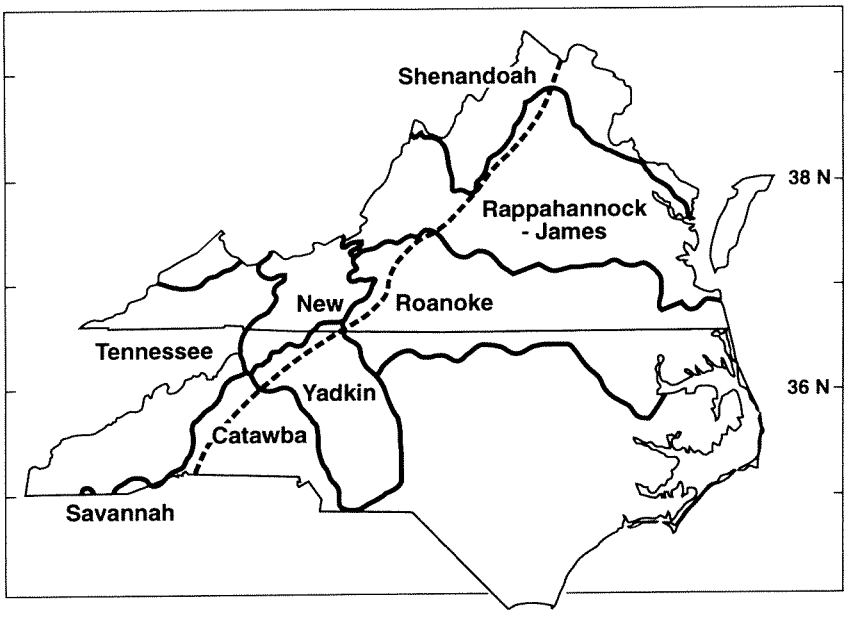

FIGURE 1.—Major drainages in Virginia and North Carolina, based on U.S. Geological Survey hydrologic units. The Rappahannock River drainage contained only a few streams along the east slope of the Blue Ridge and was combined with the James River drainage. The dashed line denotes the southeastern limit for trout.

were distributed across the region in patterns distinct for each species (Figure 2). Rainbow and brown trout were generally more common in the areas of the Pisgah and Nantahala National Forests, south of Boone, North Carolina (36°12′N), and brook trout were generally more common to the north.

Latitude.—Average latitudes of streams in the seven classes of allopatric and sympatric trout streams were significantly different (Table 2; $P = 0.0001$). Average latitude for allopatric brook trout streams was farthest north, followed by latitude for streams that supported brook trout sympatric with other species; rainbow and brown trout groups were farthest south (all significant, $P < 0.05$; Table 2).

Elevation.—Allopatric brook trout streams were expected to occur at highest elevations, followed by sympatric streams and allopatric rainbow and brown trout streams. Among the seven stream classes, elevations were significantly different ($P < 0.001$) for the region as a whole (Table 2), but the pattern was not as expected. Elevations of allopatric brook, rainbow, and brown trout streams were not significantly different ($P > 0.05$). Streams with sympatric populations were generally at higher elevations than streams with allopatric populations, but only streams with all three species had elevations significantly different ($P < 0.05$) from those with allopatric populations.

To determine whether this unexpected pattern was due to confounding of the effects of latitude and elevation, I repeated the analysis separately for the two states. In both cases, differences in elevation among the seven stream classes were significant (Table 2, $P < 0.05$). The pattern for Virginia streams was similar to that for the region as a whole, except that allopatric brook trout streams were on average 36 m lower than allopatric rainbow trout streams (not significant). Allopatric brook trout in Virginia were found in many

TABLE 1.—Numbers of streams with allopatric and sympatric trout and corresponding mean trout densities in North Carolina and Virginia. Streams with sympatric populations include all combinations of two or more salmonid species. Densities were significantly different (Kruskal–Wallis; $P < 0.0001$). Different letters denote significantly different mean density rank (nonparametric pairwise comparison; $P < 0.05$).

Stream class	Number of streams	Density (number/m^2)
Allopatric brook trout	392	0.044 z
Sympatric populations	252	0.026 y
Allopatric rainbow trout	242	0.025 y
Allopatric brown trout	92	0.007 x

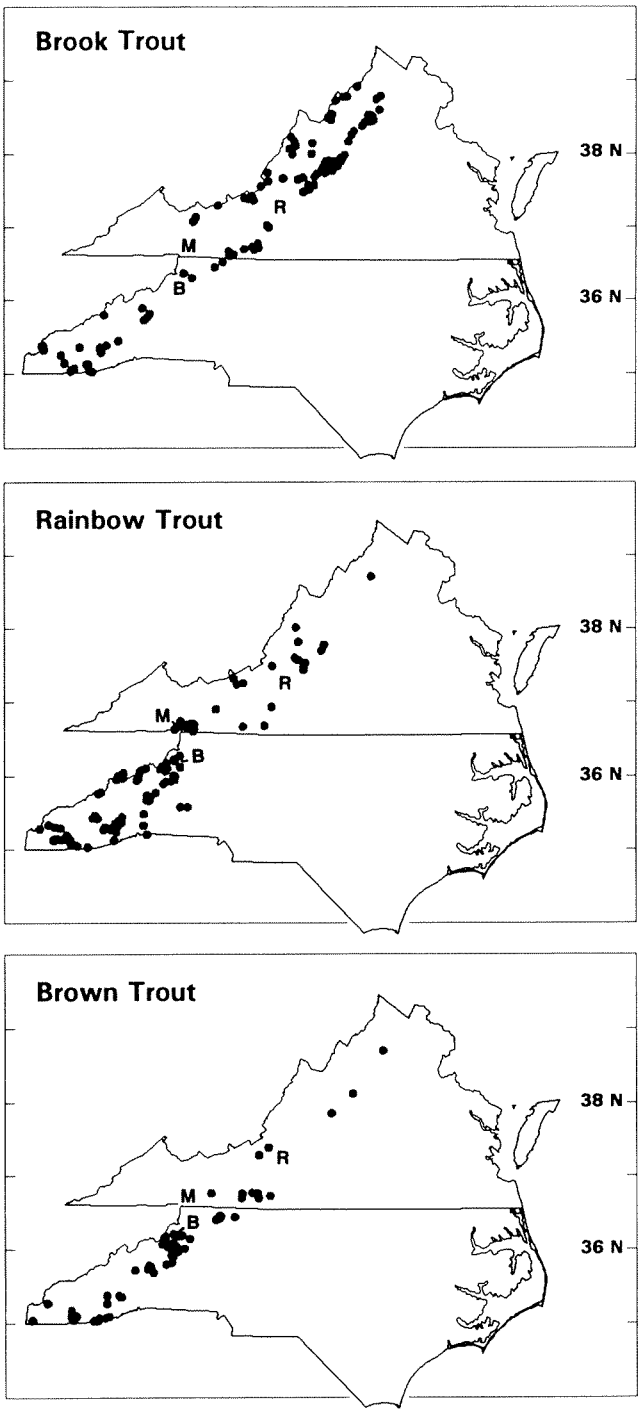

FIGURE 2.—Distributions of streams with highest brook, rainbow, and brown trout densities, defined as streams with densities in the upper 25th percentile of each species' distribution. Each dot may represent more than one stream. Locations of Roanoke (city) and Mt. Rogers, Virginia, and Boone, North Carolina, are denoted by R, M, and B, respectively.

TABLE 2.—Numbers of streams with allopatric or sympatric brook, rainbow, and brown trout—and their average latitudes and elevations—in Virginia and North Carolina. Effective elevation was calculated by equation 1. Each latitude or elevation column represents a single analysis of variance (all were significant; $P < 0.001$) and different letters denote groups that were significantly different (least significant difference; $P < 0.05$).

	Region				Virginia		North Carolina	
Trout stream class	Number of streams	Average latitude (°N)	Average elevation (m)	Average effective elevation (m)	Number of streams	Average elevation (m)	Number of streams	Average elevation (m)
Brook	392	37.2 z	689 yx	1,122 z	300	594 y	92	997 z
Brook, rainbow	68	36.7 y	748 zyx	1,092 z	45	701 zy	23	839 yx
Brook, brown	51	36.6 y	758 zy	1,079 z	28	660 zy	23	878 y
Brook, rainbow, brown	17	36.5 y	825 z	1,125 z	7	719 z	10	900 zy
Rainbow	242	36.2 x	678 yx	908 y	93	630 zy	149	707 w
Rainbow, brown	116	35.7 w	746 zyx	893 y	12	669 zy	104	755 xw
Brown	92	36.1 x	664 x	885 y	23	590 y	69	689 w

streams (300 of 508 trout streams) over a wide range of elevations (226 to 1,219 m). In North Carolina, however, allopatric brook trout streams were found at the highest elevation, significantly higher than allopatric rainbow and brown trout streams (Table 2, $P < 0.05$), and sympatric streams were found at elevations intermediate between allopatric brook and rainbow trout streams.

On average, trout streams in Virginia were significantly lower ($P < 0.001$) than those in North Carolina; average elevations (±SE) were 617 ± 11 m and 791 ± 9 m, respectively. Maximum elevations were 1,305 m and 1,646 m; and minimum elevations were 192 m and 305 m for Virginia and North Carolina, respectively. For each of the seven trout stream categories in Table 2, differences in elevation between the two states were significant ($P < 0.05$) for all but the brook–rainbow–brown trout and rainbow–brown trout sympatries.

Interaction of latitude and elevation.—Effective elevation (equation 1), which increases elevation to adjust for effects of latitude, increased more for Virginia streams than for North Carolina streams, and because brook trout streams were more common in Virginia, the adjustment also increased average effective elevation of brook trout streams for the region (Table 2). Effective elevation clearly distinguished brook trout streams (all those with allopatric or sympatric populations) from other trout streams (Table 2, $P = 0.0001$).

The distributions of allopatric trout streams along gradients of elevation and latitude were quite variable, but demonstrated the relation between trout presence and these factors (Figure 3). At all latitudes, the lowest available elevation was 0 m (sea level). The highest available elevation varied with latitude, being generally lower to the north; however, elevations exceeding 1,300 m were available as far north as 38°30′N and elevations exceeding 900 m were available to 39°N. Thus, at all latitudes, salmonids used only part of the range of available elevations. The regression lines (Figure 3) for allopatric rainbow and brown trout streams were nearly identical over the range of latitudes observed, but the regression for brook trout streams was steeper. The regression for sympatric trout streams was also significant ($P < 0.001$, $r^2 = 0.15$), and the slope (−93.6) was intermediate. Although all four regressions were significant, only the regression for brook trout explained enough variance ($r^2 = 0.59$, Figure 3) to be meaningful.

Major Drainages

Highest average densities of trout were in the two northernmost drainages (Table 3). In general, brook trout occurrence (percentage of trout streams with brook trout) and density decreased in drainages from north to south, except for the Savannah River drainage samples. Brook trout densities were significantly (nonparametric, $P < 0.05$) different between the Shenandoah and the New and Catawba River drainages; the James–Rappahannock and the New, Tennessee, and Catawba River drainages; and the Roanoke and the Catawba River drainages. Rainbow trout occurrence showed the reverse trend, increasing from north to south. Highest rainbow trout densities were in the Tennessee River and Catawba River drainages, significantly (nonparametric, $P < 0.05$) different from densities in the New River system. Brown trout occurrence also increased from north to south, but densities were low everywhere.

Within drainages, the seven trout stream classes were distributed across elevation in patterns similar to those given for the respective states in Table 2. Trout distribution in the New River and Ten-

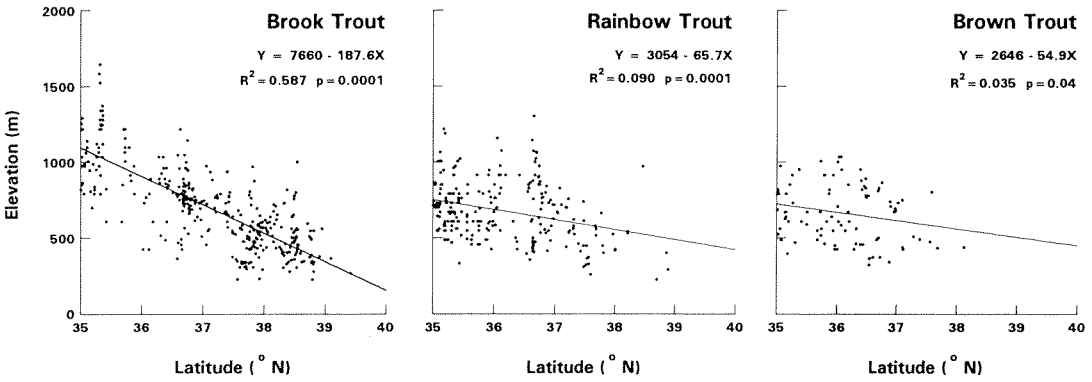

FIGURE 3.—Relationships between latitude and elevation of allopatric brook, rainbow, and brown trout streams. Each point represents one stream, and lines are least-squares regressions.

nessee River drainages, which encompass parts of both states, resembled patterns for Virginia and North Carolina, respectively. In all except the James–Rappahannock and the New River drainages, allopatric brook trout stream elevations were significantly ($P < 0.05$) greater than those of rainbow trout streams (see Figure 4). Average elevations of allopatric brook trout streams among major drainages were significantly different ($P < 0.001$) (Figure 4), and minimum and mean elevations generally increased from north to south. Elevations of allopatric rainbow trout streams were also significantly different among major drainages ($P < 0.001$) (Figure 4). There was also a general tendency for elevation of allopatric rainbow trout occurrence to increase from north to south, but highest elevations were in the New and Tennessee River drainages. These patterns were a function both of trout distributions and elevations available in each major drainage. The highest and lowest elevations were not available in all drainages; however, 90% of all trout streams occurred at elevations from 344 to 1,122 m, and all drainages, except the New River drainage (where minimum elevation in Virginia is 460 m), span this range of elevations within the boundaries of North Carolina and Virginia.

Discussion

This analysis describes the regional distribution and abundance of salmonids when stream inventories were conducted, 1975–1981. Some changes in trout distribution and abundance have no doubt occurred since then. Furthermore, conclusions about salmonid densities are limited because the sampling method was not truly quantitative. An updated inventory based on quantitative sampling methods would certainly strengthen the con-

TABLE 3.—Trout occurrences and densities in major drainages of North Carolina and Virginia. Boundaries of drainages are shown in Figure 1. Average elevations of all trout streams and numbers of trout streams within North Carolina and Virginia are given for the drainage. Occurrence is expressed as percentage of trout streams in the drainage within North Carolina and Virginia that have a given species. Among basins, densities of all trout ($P < 0.0001$), brook trout ($P < 0.0001$), and rainbow trout ($P = 0.003$) were significantly different (Kruskal–Wallis), but densities of brown trout were not ($P = 0.22$).

Drainage	Elevation (m)	Number of trout streams	Trout (all species) density (number/m^2)	Brook trout		Rainbow trout		Brown trout	
				Occurrence (%)	Density (number/m^2)	Occurrence (%)	Density (number/m^2)	Occurrence (%)	Density (number/m^2)
Shenandoah	477	64	0.047	95	0.046	12	0.009	3	0.004
Rappahannock–James	492	188	0.052	86	0.055	21	0.019	8	0.006
Roanoke	575	52	0.028	58	0.032	37	0.014	33	0.007
New	801	183	0.019	70	0.019	32	0.011	28	0.005
Tennessee	808	340	0.025	31	0.022	68	0.022	35	0.005
Yadkin	508	46	0.016	39	0.024	41	0.011	41	0.008
Catawba	560	83	0.027	17	0.007	74	0.026	46	0.009
Savannah	787	22	0.020	82	0.024	86	0.011	86	0.008

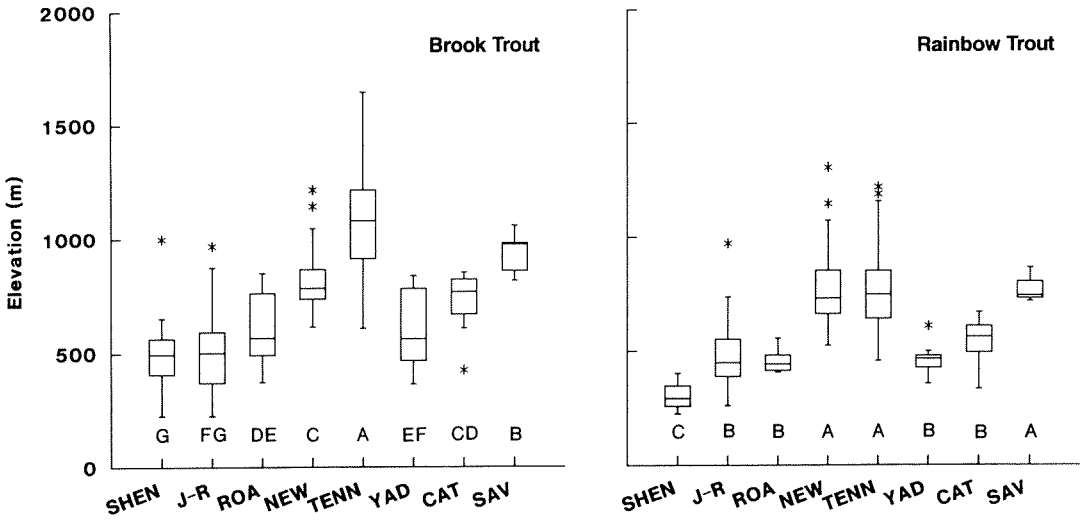

FIGURE 4.—Elevations at which streams with allopatric brook trout or rainbow trout occur in major drainages (Figure 1) of North Carolina and Virginia. Horizontal lines represent the 75th, 50th (median), and 25th percentiles; the vertical lines denote 1.5 times the interquartile range (the difference between the 25th and 75th percentiles), and asterisks represent outlying observations. Different capital letters below boxes denote significantly different mean stream elevations.

clusions. Nevertheless, some general statements can be made about trout abundance and distribution from this analysis of existing data.

Allopatric brook trout, the native condition, remained most common and abundant throughout the region, especially in Virginia. Brook trout were more likely to be found, and at higher densities, in allopatric situations (74%) than sympatric ones (26%), somewhat lower than the 53% sympatry in Tennessee (Bivens et al. 1985). Among streams with sympatric brook and rainbow trout (9% of all trout streams), neither species consistently dominated in numbers of individuals; in individual streams sympatry ranged from dominance by brook trout to dominance by rainbow trout, similar to patterns observed in Great Smoky Mountains National Park (Larson and Moore 1985). To the north, brook trout were generally found in allopatric populations, and the importance of sympatry increased to the south. Rainbow trout, the second most common and abundant species, were more common to the south and at lower elevations than brook trout. Fisheries managers have suggested that rainbow trout are more successful south of Roanoke (Mohn, personal communication) or Mt. Rogers (M. Seehorn, U.S. Forest Service, personal communication), Virginia, than they are north of these locations. The occurrence of streams with high densities of rainbow trout declined from 30% north of Boone, North Carolina, to 19% north of Mt. Rogers and 12% north of Roanoke (Figure 2), suggesting a gradual decline in rainbow trout success to the north. Brown trout had a limited distribution and low abundance throughout the region.

Based on patterns observed in the Great Smoky Mountains and neighboring areas of Tennessee (Lennon 1967; Kelly et al. 1980; Bivens et al. 1985; Larson and Moore 1985), the expected elevational sequence of trout populations, from highest to lowest, was allopatric brook trout, then sympatric populations, then allopatric exotics. This pattern held well for neighboring areas of North Carolina, but not for Virginia or the region as a whole because both latitude and elevation affect distribution. Only when both elevation and latitude were combined into a single factor, effective elevation, did a clear elevational effect on distribution emerge at the regional scale (Table 2).

In the southern Appalachians, trout are thought to occur only above 600 m of elevation, and some have suggested that brook trout are no longer found below about 900 m (Lennon 1967; MacCrimmon and Campbell 1969; Bivens et al. 1985). However, 43% of the minimum elevations for brook trout in 135 Tennessee streams are below 900 m, and brook trout are found in several streams below 600 m (Bivens et al. 1985). Although these limits may generally hold for the most southern portions of the southern Appalachians, trout occur at lower

elevations in most of North Carolina and Virginia (Figure 3). Based on visual inspection of Figure 3, minimum elevation for allopatric brook trout probably declines from about 700 m at 35°N to level off at about 200 m north of 37°30′N (near Roanoke). In a similar analysis of these and neighboring state stream inventories, Meisner (1990) selected minimum elevations at which brook trout occur in watersheds and also found a negative relation between latitude and elevation: minimum elevation decreased from 640 m at 34°40′N to 0 m at 39°12′N.

In my regional analysis, brook trout did tend to occur at higher elevations than rainbow or brown trout, but within major drainages and across the region, there was considerable overlap in distribution of species by elevation. Although in individual streams, brook and rainbow trout may segregate by elevation, often with a zone of sympatry between allopatric zones, critical elevations differ among streams, even within the same watershed. For example, in 1975 along the main stem of the East Prong Little River, allopatric rainbow trout were found up to 1,265 m and allopatric brook trout were found only above 1,329 m (Kelly et al. 1980). Yet, in all eight tributaries for which elevations were reported, no rainbow trout were reported above 1,219 m, and in one tributary, allopatric brook trout were found at 518 m (Kelly et al. 1980). Thus, minimum and maximum elevations observed for trout species in one stream are not always repeated in nearby streams.

To explain these regional landscape patterns of abundance and distribution, one must examine patterns and processes within streams because in a hierarchy of systems, explanations for patterns observed at one level are found at the next lower level (O'Neill 1988). Replacement of brook trout by introduced rainbow trout has received the most attention as a factor affecting distribution of salmonids in areas of North Carolina and Tennessee near Great Smoky Mountains National Park (Moore et al. 1983, 1986; Bivens et al. 1985; Larson and Moore 1985). Although effects of interspecific competition between brook and rainbow trout have been difficult to demonstrate in streams, many workers cite interactions of competition with habitat preferences, including temperature requirements, as mechanisms to explain replacement of brook trout (Hearn 1987; Fausch 1988, 1989; Lohr and West 1992). Other factors have been cited to explain replacement of brook trout but remain to be tested (Fausch and White 1981; Waters 1983; Bivens et al. 1985). Alternatively, stream gradient (Larson and Moore 1985; Fausch 1988, 1989) and physical barriers (Bivens et al. 1985) maintain separation of species in some streams.

Conversely, the regional pattern of trout distribution constrains pattern and process at the level of individual streams (O'Neill 1988). For landscapes, a major research task is to identify heterogeneities, whether patches or gradients. Here, gradients of latitude and elevation contributed to the overall trout distribution pattern, probably through influence on stream temperature. That influence was stronger for brook trout than for the other two trout species (Figure 3). Although these trout streams were mainly on forested land, present and historical land use, which also varies with elevation, may influence present trout distributions in the region (Flebbe et al. 1988). Effects of large-scale factors can be modified by stream conditions, including riparian vegetation and cover, or by interspecific interactions that are apparent as noise (variance) at the regional level (Figure 3). Tests of mechanisms must occur at the level of the stream system, but they must include a broad range of conditions observed for the region. Relative importance of multiple causal factors (e.g., temperature, competition, habitat preferences) may differ across the region; additional research in areas removed from the Great Smoky Mountains would be needed to further explore generality of the brook trout replacement process.

A regional perspective, represented by analyses such as this one, provides the context in which results of site-specific research might be applied to trout management. Management activities, including habitat management, stocking, and angling regulations, can be designed to enhance the distributional patterns of trout species. Restoration of high-elevation brook trout streams (Moore et al. 1983, 1986; Larson and Moore 1985) is appropriate in areas of North Carolina and Tennessee near the Great Smoky Mountains National Park. Rainbow and brown trout were most successful in lower elevations of North Carolina; thus, opportunities to maintain fisheries for these species in the region are best in these areas. A different approach to management may be more appropriate to the north, where rainbow and brown trout are less common and brook trout remain most common and abundant at all mountain elevations. Here, rainbow and brown trout fisheries may be limited to a few special cases, and native brook trout fisheries may be emphasized with less effort than required to the south.

The southern margin of trout in Virginia and North Carolina is quite broad and diffuse, a composite of responses by three salmonid species to gradients of latitude and elevation, which influence stream conditions; interstream variability is superimposed on these conditions. Research based on individual case studies (e.g., Moore et al. 1983, 1986; Larson and Moore 1985) can be extrapolated only to limited areas unless the generality of results can be shown. With a regional-scale view of trout streams in Virginia and North Carolina, differences across the region were identified and a more comprehensive view of trout distribution and abundance in the region emerged.

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