Transactions of the American Fisheries Society 135:1371–1382, 2006

DOI: 10.1577/T05-217.1

[Article]

Spatial Modeling to Project Southern Appalachian Trout Distribution in a Warmer Climate

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Abstract.—In the southern Appalachian Mountains, the distributions of native brook trout *Salvelinus fontinalis* and introduced rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* are presently limited by temperature and are expected to be limited further by a warmer climate. To estimate trout habitat in a future, warmer climate, we produced a regional map of wild trout habitat based on information from stream samples, expert knowledge, and suitable land cover. We then developed a quantile regression model of the elevation–latitude boundary for the present distribution of trout; this constitutes a more direct, spatially explicit approach to modeling trout distribution than the use of thermal limits. In combination with a lapse rate model, the boundary model was used to project future wild trout distributions over a range of higher temperatures. If the predictions of the Hadley Centre global circulation model (GCM) are assumed, about 53% of trout habitat would be lost; if the more extreme Canadian Centre GCM is used, 97% would be lost. With increasing temperature, fragmentation would increase, leaving populations in small, isolated patches vulnerable to extirpation because of the decreased likelihood of recolonization. The regional trout habitat map and the models produced here were useful for making these predictions, and the map could be used for assessing the impacts of other regional stressors.

Stream temperature is a basic limiting factor that defines suitable habitat for salmonids, which require relatively low temperatures (Magnuson et al. 1979). Average air temperature in the United States has increased by about 0.6°C over the last century; due to increasing levels of greenhouse gases, primarily carbon dioxide, average temperature may increase by another 3–5°C during the next 100 years (NAST 2000). Climate warming represents a threat to the long-term persistence of wild trout species within the southern Appalachian Mountains; trout species in this area are at the southern limits of their range and are thus already limited by temperature. Suitable trout habitat will probably shrink in this region if the climate warms substantially.

Three species of trout live in the southern Appalachians (i.e., mountain areas of Georgia, South Carolina, North Carolina, Tennessee, and Virginia): the native brook trout *Salvelinus fontinalis* and the introduced rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta*. Temperature requirements of the three trout species are similar (Eaton et al. 1995), but distributions of the three species are patchy and overlap to some degree. Introduced trout have replaced brook trout in many streams, often relegating brook trout to higher elevations (Larson and Moore 1985). Adjacent streams may have different species at the same elevation (Lennon 1967), and zones of sympatry are common (Flebbe 1994). Therefore, for purposes of this study, we consider the three species as a single trout guild.

Stream temperature decreases predictably with increasing elevation in the mountains, largely due to the temperature lapse rate of the atmosphere (i.e., the rate at which air temperature declines with increasing altitude) (Bolstad et al. 1998; Isaak and Hubert 2001). Thus, elevation and temperature can be used interchangeably in delineating regional trout habitat in mountain areas. In this study region, which extends over 4.6° of latitude (from 34.5°N to 39.1°N), limiting temperature for trout distribution is a function of both elevation and latitude. All three species of trout are distributed along latitudinal and elevational gradients in the region; the average elevation at which trout live

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Received August 31, 2005; accepted April 12, 2006
Published online October 2, 2006

declines with increasing latitude, more steeply for brook trout than for rainbow trout and brown trout (Flebbe 1994). These relationships can be modeled to delineate both current trout elevation limits and projected limits in a warmer climate.

The amount of temperature increase is not uniform across the planet, and various global circulation models (GCMs) predict different magnitudes of temperature increase. For the Southeast, the Hadley Centre GCM projects mean annual temperature increases of about 2.3°C and the Canadian Centre GCM projects a 5.5°C increase by the year 2100 (Burkett et al. 2001). Effects of increased air temperature on stream water temperature will vary from site to site, depending on such factors as the degree of groundwater influence, amount of shading by watershed and riparian vegetation, and watershed aspect.

If temperatures in the southern Appalachians increase, minimum elevations at which trout can live would increase for much of the area. Based on his own model, Meisner (1990) predicted that the 3.8°C increase in temperature predicted for the mid-21st century by the Goddard Institute for Space Studies model would increase the minimum elevation for brook trout distribution by up to 714 m and shrink the brook trout range, but he was unable to apply his model to a trout stream inventory to estimate loss of habitat. Habitat for trout would also become more fragmented as the range shrinks into "islands" near the tops of mountains (Flebbe 1993, 1997). Clark et al. (2001) predicted that trout habitat in the region would decline by about 20% or 80% with a 1.5–2.5°C temperature increase, depending on whether an individual-based model or a simple temperature model, respectively, was used.

Most models of trout distribution in a warmer climate are based on the analysis of trout range in an area (Meisner 1990; Keleher and Rahel 1996; Rahel et al. 1996; Clark et al. 2001), assuming that this range is homogeneously suitable trout habitat. However, trout habitat is associated with mature forest and not with human-dominated land cover (Flebbe et al. 1988), and fragmentation of suitable land cover on the landscape will probably exacerbate effects of climate change (Opdam and Wascher 2004). Land cover (herein, we use "land cover" in place of "land cover and land use") information can be combined with trout distribution range information to map trout habitat in the region to more accurately assess how trout habitat would shrink in a warmer climate.

Other climate change impacts on the stream environment of trout are likely but will not be considered in this analysis. Precipitation changes are expected, but the magnitude and direction of changes are not clear. The Hadley Centre GCM predicts increases of 20%, and the Canadian Centre GCM predicts decreases of 10% for the Southeast by 2090 (Burkett et al. 2001). Effects on streamflow are likewise unclear. Although in some streams hydrologic changes can be as important to trout as temperature (Jager et al. 1999), such changes are likely to vary among streams within the region, and we were unable to incorporate them in these regional models. The following effects are indirect and difficult to model: changes in riparian zone vegetation that alter inputs of allochthonous material, changes in macroinvertebrate community structure and metabolism that represent changes in trout food availability, and changes in distribution of other fish species that alter interspecific interactions within the stream fish community.

The objectives of this research were to (1) produce a regional model of minimum elevation at which trout presently occur from a map of trout habitat in the southern Appalachian Mountains; (2) develop a regional prediction of trout habitat that may be expected for a range of temperature increases; and (3) compare current fragmentation of trout habitat to fragmentation of trout habitat in a warming climate.

Methods

General approach.—The first step in producing such regional analyses for trout is to create a map that depicts current trout habitat in the southern Appalachians. This analysis requires information about trout distribution that has a large extent and that is moderately fine grained (sensu Turner et al. 1989). Traditionally, information about fish distributions has been reported in the form of (1) range maps, which have a large extent and are very coarse grained, or (2) descriptions of habitat use in streams, which have a small extent and are fine grained. Inventories of point samples over a large geographic area are of limited use because a very small portion of the total stream length is sampled. We combined information from range maps, point samples, expert opinion, and land cover maps to produce a map of fish distribution over a large extent with enough detail to permit moderately fine-grained analysis.

Our approach for modeling changes in trout distribution in a warmer climate (Figure 1) differed from that used in previous studies primarily in how we determined limits to the current distribution. In several studies, suitable trout habitat was determined by estimating water temperature as a function of elevation and latitude at sample sites where trout were found (Meisner 1990; Keleher and Rahel 1996; Rahel et al. 1996). Rahel et al. (1996) and Keleher and Rahel (1996) identified trout habitat for Wyoming and the

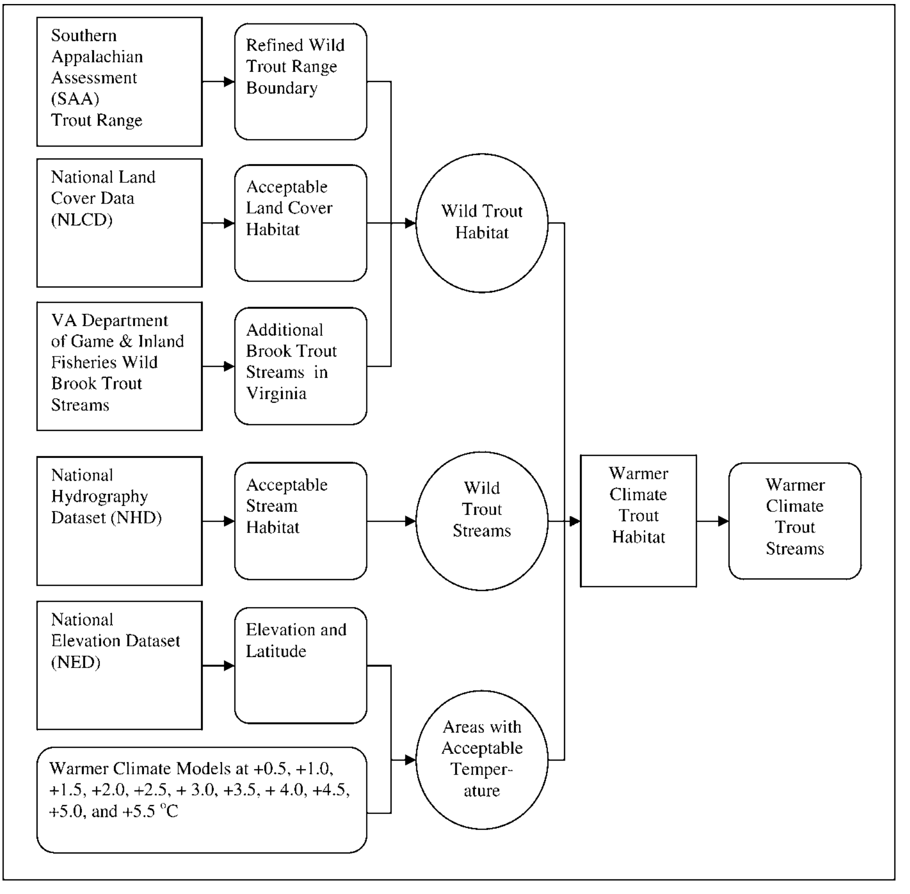

FIGURE 1.—Simplified flow chart of the processes used to develop trout habitat inventory coverage and to model the impacts of temperature changes on trout distribution in the southern Appalachian Mountains.

Great Basin, respectively, by selecting all areas that were cooler (higher) than their empirically derived maximum summer temperature. However, thermal limits for trout can vary across a region (Huff et al. 2005). Our approach also differed from that of Clark et al. (2001), who either extrapolated individual-based models of trout to all streams in 101 watershed elevation zones or simply noted whether suitable temperatures existed in these zones.

For this study, we lacked surface water temperature data that corresponded to trout survey samples at the lower elevation boundary. Furthermore, we did not know whether trout were limited by maximum summer temperature or some other aspect of temperature. We used current trout habitat, described above, and model elevation as a function of latitude at the lower distributional boundary (i.e., a boundary model). We assumed that this distribution boundary for trout in the southern Appalachians, at the southern range limit of trout, is largely determined by temperature, which is a function of elevation and latitude in mountain areas (Meisner 1990; Isaak and Hubert 2001). Previous models of trout distribution in the southern Appalachians based on minimum elevation at latitude have been fitted visually (Meisner 1990), but less subjective methods are now available.

Other factors affect the lower elevation boundary of this trout distribution. Some factors, such as relief, aspect, gradient, land cover, and riparian vegetation, may modify stream temperature in a particular stream (Brown and Krygier 1970; Swift and Messer 1971; Isaak and Hubert 2001). Other factors, such as instream habitat and interspecific interactions, may eliminate trout from portions of streams that are otherwise thermally suitable. Geography, agricultural and developed land use, and past disturbance operate to increase minimum elevation for trout habitat in any particular stream, and factors such as stocking or hypolimnetic release of water from reservoirs may counteract zoogeography to decrease minimum elevation for trout habitat in some streams. This situation, in which a response is limited by one factor that is modified by other, often unknown factors (Kaiser et al. 1994), has been called a "triangular distribution" (Maller et al. 1983) or a "wedge-shaped pattern" (Terrell et al. 1996). Recognizing that limiting relations are not always linear and the resulting distributions might be "humped," Thomson et al. (1996) proposed the term "factor-ceiling distribution"; our example is the mirror of this, the "factor-floor distribution." Simple regression models are not appropriate to describe the relation between a limiting factor and the response (Kaiser et al. 1994). Quantile regression is a statistical method that has been developed for modeling these limiting factors (Kaiser et al. 1994; Terrell et al. 1996) and was used in our analysis to model the lower distribution boundary for trout in the region.

To model changes to this boundary resulting from a warmer climate, we used temperature lapse rate to convert temperature change to a change in minimum elevation at which trout might survive. The various GCMs predict different endpoints for the region (e.g., 2.3°C for the Hadley Centre GCM and 5.5°C for the Canadian Centre GCM by 2100: Burkett et al. 2001). Rather than limit trout distribution predictions to these endpoints, we made predictions for 0.5°C increments of temperature up to 5.5°C.

Constructing a trout habitat map.—We started with the trout range (Figure 1) created by one of us (P.A.F.) for the Southern Appalachian Assessment (SAA; SAMAB 1996). To create the SAA trout range, we used state and federal inventory data (Fatora and Beisser 1980; Kelly et al. 1980; Mohn and Bugas 1980; Bonner 1983; Larson and Moore 1985; Strange and Habera 1995), state water quality data, and expert opinion.

We established an arbitrary northwestern boundary where major drainages (eight-digit U.S. Geological Survey [USGS] hydrologic units) tend to coincide with the Virginia–West Virginia state line. Most of this state line is also a boundary either between the North Fork Shenandoah and Potomac River headwater drainages or between the upper James and Greenbriar rivers. The state line bisects the middle New River and excludes small headwater sections of the North Fork Shenandoah and upper James River drainages that lie in West Virginia. We included a few headwater streams in Virginia sections of the South Branch Potomac River and the Big Sandy River, which flow into West Virginia and Kentucky, respectively.

For this study, we superimposed the SAA trout range on a map constructed from the Environmental Protection Agency (EPA) River Reach File 3 (RF3) data, which is based on the 1:100,000-scale USGS digital line graph hydrography data (SAMAB 1996). We consulted more than 30 coldwater fisheries experts, state and federal fish biologists, and university researchers in the southern Appalachians; they were asked to redraw the boundary based on their field experience with streams on the map. When consulting experts, we asked them to use their knowledge of where trout were in the late 1990s based on sampling and actual experience and not on historical distributions, putative minimum elevations (such elevations do not apply uniformly across the region: Meisner 1990; Flebbe 1994), or personal beliefs or speculation about trout occurrence. The James and New rivers are large and do not support trout where they flow through portions of the trout range, although many of their tributaries are trout streams. These rivers are probably effective barriers to trout migration due to physical conditions and the presence of other predatory fish. In consultation with state biologists, we excluded these sections of large rivers and about 400 m on each side of these sections. After the wild trout range map was completed, the experts were invited to review our results and a few minor modifications were made to reach consensus. The refined trout range boundary was digitized by hand and adjusted to eliminate inappropriate fragmentation of streams on the RF3 map. This map, constructed by use of ArcInfo software, constitutes the wild trout range boundary map (Figure 1).

This wild trout range was known to include many streams that do not actually have trout. Wild trout predominantly occur in southern Appalachian streams within forested watersheds rather than in streams associated with agricultural and developed human land uses (Flebbe et al. 1988; Harding et al. 1998). We used the 1992 National Land Cover Data Set of USGS and EPA (MLCD Consortium 2001) to identify the following areas within the wild trout boundary map that were considered to be unsuitable for trout because surrounding land cover was not forested: developed (classes 21–23); barren (31–33); orchards, vineyards, etc. (61); grasslands and herbaceous (71); and herbaceous planted and cultivated (81–85). All other land covers were considered to be acceptable habitat (Figure 1). We merged habitat and nonhabitat patches that were smaller than 1 km^2 with surrounding patches to produce the wild trout habitat map (Figures 1, 2).

To further refine trout habitat and for subsequent analyses of streams, we used the National Hydrography Data (NHD) 1:24,000-scale stream maps (1:100,000 scale where higher resolution was not available). All canals, ditches, pipelines, lakes, ponds, and reservoirs were removed. Reservoirs, lakes, and ponds are either stocked directly or have trout that migrate incidentally from populations in tributary streams (SAMAB 1996).

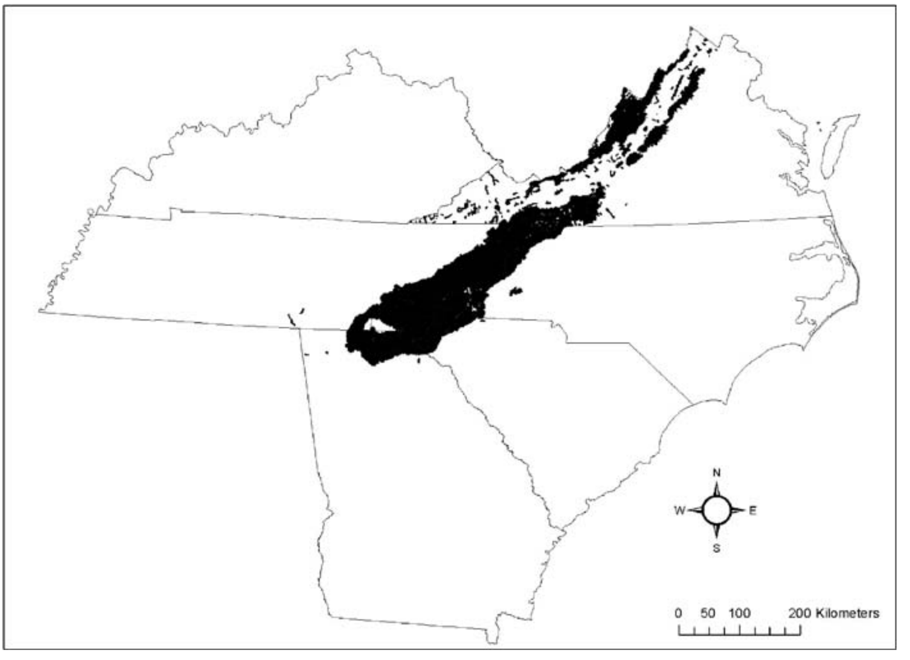

FIGURE 2.—Map depicting wild trout habitat (shaded area) in the southern Appalachian Mountains.

We added some isolated wild trout streams, primarily self-sustaining tailwater and spring-fed streams (WVDNR 1989; TWRA 1994; GADNR 1995; Mohn 1995), and a few wild brook trout streams identified in more recent data obtained from the Virginia Department of Game and Inland Fisheries Coldwater Stream Survey database (M. Hudy, U.S. Forest Service, personal communication). Buffers of 100 m on each side of these added streams were included on the habitat map (Figure 1). Again, patches less than 1 km^2 were eliminated to form the final wild trout habitat map (Figure 2).

Modeling the trout boundary.—In this mountain landscape, changes in temperature are modeled by surrogate changes in elevation. The first step was to model the relationship between elevation and latitude at the trout boundary. We selected the 489 points where streams in the RF3 map cross the range boundary described above, and we created a data set of elevation (m) and latitude (decimal degrees) for each point (Figure 3). These data were used to model the elevation–latitude space that limits trout at the boundary.

Quantile regression is used increasingly to model effects of a limiting factor where other limiting factors might also be acting and is superior to traditional least-squares regression methods (Terrell et al. 1996; Scharf et al. 1998; Cade et al. 1999; Dunham et al. 2002; Cade and Noon 2003). We knew a priori that other factors might restrict trout to elevations above the elevation–latitude boundary that represents their thermal tolerance. The lower quantiles (τ = 0.05, 0.10) represent thermal limitations at a lower elevation boundary, or

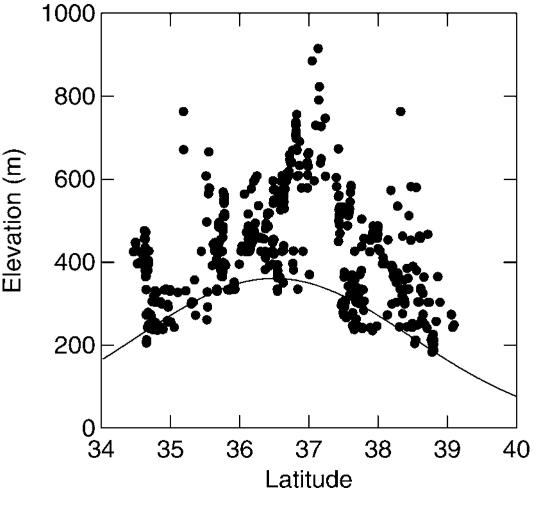

FIGURE 3.—Relationship between the elevation and latitude (°N) at which streams cross the wild trout boundary on a map of the southern Appalachian Mountains (n = 489 points). The curved line reflects the following quantile regression model (τ = 0.10): elevation = exp[−163 + (9.23 × latitude) − (0.126 × $latitude^2$)].

TABLE 1.—Summary results of thermal models describing the effect of climate warming on trout distribution in the southern Appalachian Mountains. Base habitat is the present-day wild trout habitat of Figure 2. The remaining rows represent the warmer climate habitats for the given value of ΔT in equations (2) and (3).

Habitat	Total area (km^2)	Area of largest patch (km^2)	Number of patches: >1,000 km^2	100–1,000 km^2	10–100 km^2	Total	Total stream length remaining (%)
Base habitat	42,104	33,002	3	4	16	141	
+0.0°C	41,882	32,912	3	4	14	131	99
+0.5°C	40,367	31,688	4	3	15	119	93
+1.0°C	37,714	29,849	3	3	17	120	85
+1.5°C	33,016	25,672	3	7	23	128	71
+2.0°C	26,617	10,751	3	7	37	201	52
+2.5°C	19,849	6,282	3	12	46	182	35
+3.0°C	13,795	3,803	2	19	40	168	21
+3.5°C	9,114	3,042	1	12	42	141	12
+4.0°C	5,731	1,137	2	9	42	134	7
+4.5°C	3,384	893	0	8	20	99	4
+5.0°C	1,973	651	0	3	17	66	2
+5.5°C	1,120	312	0	3	14	42	1

floor; additional factors further limit trout to higher elevations in some streams. The parabolic shape of the points in Figure 3 dictated a quadratic model. A quadratic model, however, produces negative elevation estimates, so we selected an exponential quadratic model form. Quantile regression estimates for the boundary model and rank-score tests were estimated using the BLOSSOM software package (Cade and Richards 2001). The model $Y = \exp[(b_0 + b_1X + b_2X^2 + \varepsilon)]$, where Y is elevation, X is latitude, and ε is a random error, was estimated in its linearized form: $\log_e Y = b_0 + b_1X + b_2X^2 + \varepsilon$. Confidence intervals were estimated by inverting quantile rank scores for τ values between 0.05 and 0.95 (Cade et al. 1999).

Modeling climate change predictions.—The approach for predicting response to climate change is similar to that used for streams in Wyoming (Rahel et al. 1996) and the Great Basin (Keleher and Rahel 1996). Climate change projections from GCMs are changes in air temperature, but trout respond to changes in water temperature. Several existing regression models relate air temperature to ground or surface water temperature (e.g., Meisner 1990; Stefan and Preud'homme 1993; Rahel et al. 1996). The slopes of these linear models can be used to predict change in water temperature from air temperature changes between 5°C and 25°C (Mohseni et al. 2003). Several analyses of USGS gauging station data have shown that a 1.0°C change in air temperature corresponds to a stream and river water temperature change of 0.9–1.0°C (Meisner 1990; Stefan and Preud'homme 1993; Pilgrim et al. 1998); lower values occur in areas where temperatures exceed 25°C (Mohseni and Stefan 1999). Meisner (1990) determined that at USGS gauging stations in the southern and central Appalachians, a 1°C change in air temperature corresponds to a 0.94°C change in water temperature, but that author used a value of 1.0 to predict change in groundwater temperature. For our analyses, we used a factor of 1.0 because estimates converge on this value for temperatures in the range of concern for trout, and its use is supported by physical theory (Mohseni and Stefan 1999).

To convert air temperature change to change in minimum elevation, we used an empirical relation equating 188 m of elevation change to 1°C change in air temperature, based on air temperature data from the southern Appalachians (Meisner 1990). This value (188 m/°C) corresponds to a temperature lapse rate of 5.3°C/km, midway between the lapse rates of 7°C/km and 3°C/km for maximum and minimum temperatures, respectively, in the southern Appalachian region (Bolstad et al. 1998). We predicted the minimum elevation at which trout can survive with a warmer climate model by adding the temperature change model to the boundary model (Figure 1). Effects of 0.5–5.5°C increases on suitable trout habitat were assessed in increments of 0.5°C. The warmer climate models were applied to the National Elevation Dataset (NED) to identify areas of acceptable temperature within the present trout habitat area that would remain in a warmer climate (Figure 1). Patches smaller than 1 km^2 were excluded from analysis. Projected trout habitat areas were used to select streams from the NHD coverage and predict remaining stream length for the range of temperature increases (Table 1).

Results

The current distribution of wild trout streams (Figure 2) comprises some large areas of relatively intact habitat and others that are smaller and more fragment-

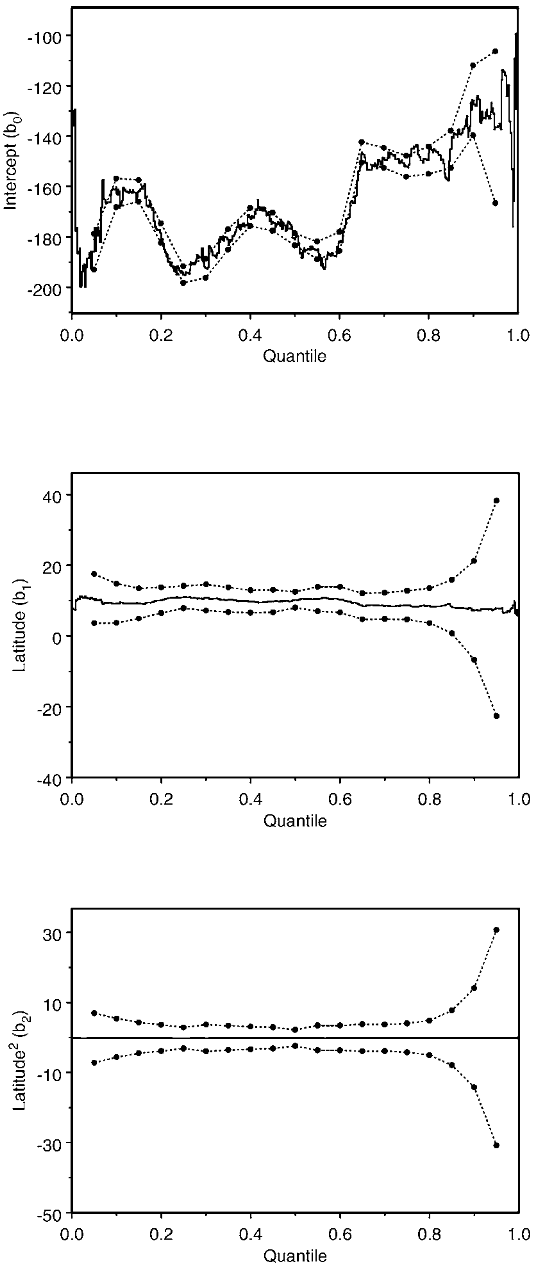

FIGURE 4.—Estimates of the parameters from quantile (τ) regressions of minimum elevation as a function of latitude for the wild trout boundary in the southern Appalachian Mountains. Estimates for all τ values are shown as solid step functions. Dashed lines connect the endpoints of 90% confidence intervals calculated at τ values between 0.05 and 0.95 (in increments of 0.05).

ed, especially in Virginia. We identified 141 patches that totaled 42,104 km^2 of habitat area (Table 1).

We selected the quantile regression model for a τ value of 0.10, based on inspection of Figures 3 and 4; at τ values of 0.10 or less, the confidence intervals become wider and the estimates of coefficients lack neighborhood stability (Figure 4). The boundary model was

$$\text{Elevation} = \exp[-163 + (9.23 \times \text{latitude}) - (0.126 \times \text{latitude}^2)]. \quad (1)$$

An adjustment was made for the areas south of 34.6°N, the southern end of wild trout distribution in the region, where the boundary runs primarily east to west and the quantile regression model fit becomes poor (Figure 3). We set the boundary at an elevation of 398 m, the 0.10 quantile for the boundary data points south of 34.6°N. When these boundary models were applied to the NED (Figure 1), the resulting map coincided reasonably well with the trout habitat boundary map and the estimated trout habitat area constituted over 99% of the current habitat area (Table 1). Combining this boundary model with the temperature change model, we obtained the following equations for estimating areas suitable for trout:

$$\text{Elevation} = \exp[-163 + (9.23 \times \text{latitude}) - (0.126 \times \text{latitude}^2)] + (188 \times \Delta T) \quad (2)$$

for latitudes greater than 34.6°N and

$$\text{Elevation} = 398 + (188 \times \Delta T) \quad (3)$$

for latitudes less than or equal to 34.6°N; ΔT is change in temperature (°C).

Projected trout habitat areas for temperature increases of 0.5–5.5°C decline until very small fragmented areas remain (Figure 5; Table 1). Likewise, stream length suitable for trout declines with increasing temperature (Table 1). With a 3°C warming, the models project a 67% loss of habitat area and a 79% loss of stream length. Suitable habitat is eliminated almost completely from Virginia at an increase of 4.5°C (Figure 5). At an increase of 5.5°C, the largest remaining refuges are in the peaks of the Great Smoky Mountains and the Blue Ridge Mountains of North Carolina.

The remaining trout habitat becomes more fragmented than it is at present. With increasing temperature, the largest trout habitat patch becomes progressively smaller (Table 1). Presently, there are several large areas of habitat greater than 1,000 km^2. At increased temperatures, these large patches break up

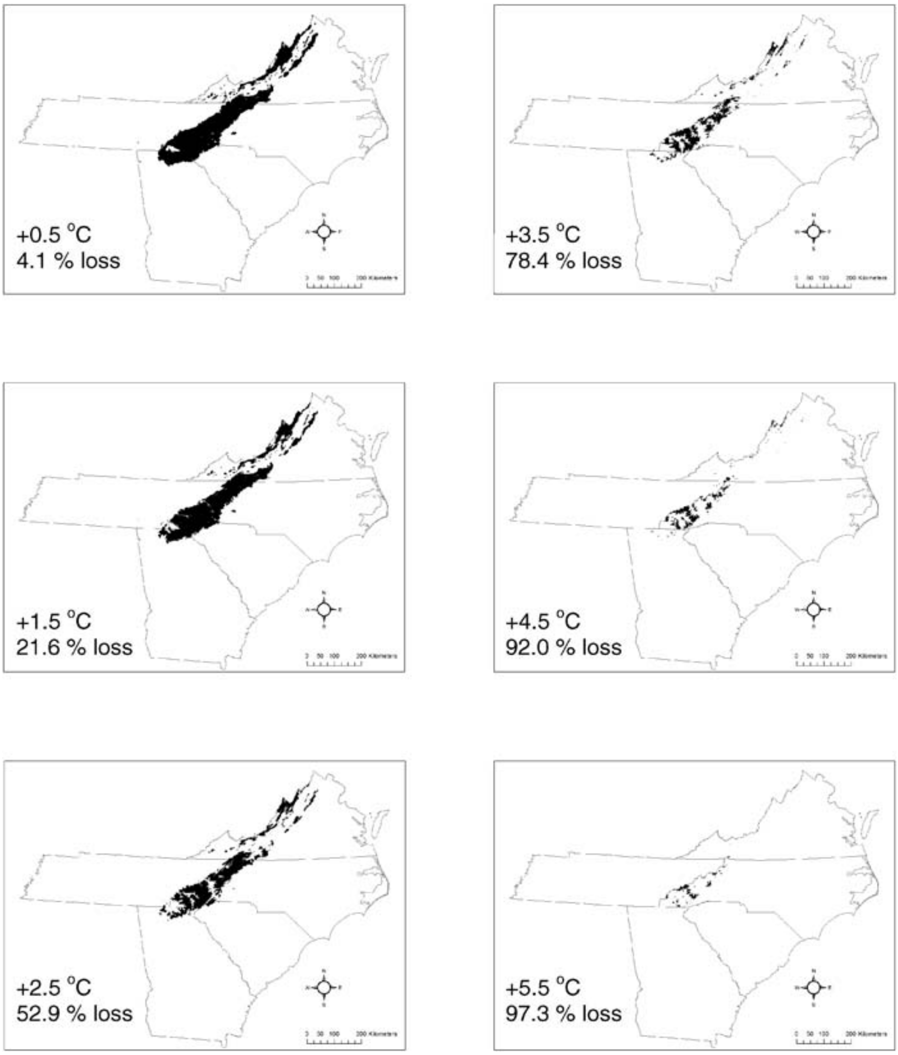

FIGURE 5.—Maps of projected wild trout habitat in the southern Appalachian Mountains under temperature increases of 0.5–5.5°C (1.0°C increments). The shaded areas are those that remain above the projected minimum elevation. The percentages reflect losses from the baseline habitat area in Figure 2. The bottom two panels correspond to Hadley Centre (left) and Canadian Centre (right) global circulation model projections.

and eventually disappear. Intermediate-sized patches of 100–1,000 km^2 and smaller patches of 10–100 km^2 become more common and then decline in number as larger patches are broken up, and eventually even the smallest patches disappear.

Discussion

Current Trout Distribution

The wild trout habitat of Figure 2 is best considered potential habitat because it includes areas, notably on private lands or small headwater streams, where trout are not inventoried and presently may or may not have trout. Some streams within our wild trout habitat area are stocked; some streams, particularly small headwater streams, do not contain trout. Our habitat map is more detailed and fragmented than previous distribution maps (Meisner 1990; Flebbe 1997). Meisner (1990) fitted his lower stream boundary visually on a linear plot of elevation versus latitude and assumed that all land above the boundary was suitable for trout, regardless of land cover. Although Flebbe (1997) included only suitable land cover in trout habitat, the original range map was less detailed than used here.

The present-day distribution of trout habitat is already fragmented (Table 1; Figure 2). Some fragmentation is due to topography and drainage patterns in the southern Appalachian areas where trout are found. Presence of unsuitable land cover also fragments trout distribution within watersheds. Land cover changes and forest harvest practices often increase stream temperature by removing streamside vegetation (Brown and Krygier 1970; Swift and Messer 1971). Concomitant with these land cover changes are stream habitat changes (e.g., removal of habitat structure, road building, channelization) and increased angling and stocking programs that make streams unsuitable for wild trout. These factors now limit the distribution of wild trout to higher elevations in the southern Appalachians (King 1937; Kelly et al. 1980; Bivens et al. 1985; Larson and Moore 1985; Meisner 1990; Flebbe 1994).

The Boundary Model

The quantile regression method proved useful for directly modeling the lower elevational boundary for trout. The method was not sensitive to the scatter in Figure 3, which represents other limiting factors, and the resulting map matched the current habitat reasonably well (+0.0°C versus base habitat in Table 1). With this approach, we did not make assumptions about what particular temperature limits trout distribution in the region. That temperature limits the distribution of coldwater fishes is well-established, but a standard thermal limit is unlikely (Rahel 2002). Keleher and Rahel (1996) and Rahel et al. (1996) assumed that mean July air or stream temperature corresponds to the thermal maximum tolerance of trout. However, using a similar measure of temperature in Oregon streams, Huff et al. (2005) found that the upper limit for rainbow trout differed among mountain regions. Thermal maxima derived from laboratory studies are less-than-ideal predictors of where trout can exist in field settings (Eaton et al. 1995; Schrank et al. 2003). Trout can exist for short periods of time (hours) at higher temperatures if they also experience daily cycling to lower temperatures (Johnstone and Rahel 2003; Schrank et al. 2003). In some cases, trout migrate to thermal refuges (Nielsen et al. 1994), but in others they do not (Schrank et al. 2003).

We still assumed that temperature limits the distribution of trout, but we did not specify the temperatures at which limitation would occur. As a surrogate for temperature, elevation integrates thermal conditions, capturing the effects of temperature limitation over annual cycles and multiple years. Further, we allowed the thermal limit to vary with latitude, which is desirable for several reasons: each of the three species has a slightly different thermal limit (Eaton et al. 1995); each species' distribution differs across latitudes (Flebbe 1994); and trout at the southern portion of our region may be more acclimated to warmer temperatures than northerly situated trout. Brook trout of the putative southern strain, more common in Tennessee and North Carolina than in the other states (SDAFSTC 2005), may tolerate slightly higher temperatures better than northern-strain brook trout. Regression lines that represent the relation between elevation and latitude for each trout species cross at 37.8°N; south of this latitude, rainbow trout and brown trout become more common and are found at lower elevations than are brook trout (Flebbe 1994). Thus, the "humped" distribution of boundary elevations in Figure 3 is not unexpected.

Trout Distribution in a Warmer Climate

Trout habitat and stream length decreased nonlinearly with increasing temperature (Table 1; Figure 5). If predictions of the Hadley Centre GCM are assumed, 53% of total trout habitat area and 65% of stream length would be lost, whereas the more extreme Canadian Centre GCM predictions indicate losses of 97% and 99%, respectively. The greater detail in the current wild trout distribution (Figure 2) resulted in a more detailed, fragmented distribution in a warmer climate (Figure 5) than was reported by Meisner (1990) for brook trout in the southern Appalachians. For a 3.8°C increase in temperature, Flebbe (1993) predicted an 89% loss of brook trout streams with Meisner's (1990) model, which is near the 78–86% loss predicted by our model for a 3.5–4.0°C temperature increase. Our prediction of a 22–53% trout habitat decline for a temperature increase of 1.5–2.5°C is closer to the 24% and 16% declines for brook trout and rainbow trout, respectively, predicted from extrapolation of individual-based models than to the 80% decline predicted by a simple temperature-based habitat estimate (Clark et al. 2001).

As the remaining habitat for trout becomes more fragmented, only small refuges in headwater streams at the highest elevations will remain. When patches become isolated (Figure 5), the possibility of trout extirpation in the region increases. Small populations in isolated patches can easily be lost, and in a warmer climate common local extinctions may become irreversible as avenues for recolonization are eliminated. Although these species would probably remain viable in other parts of their ranges, loss of habitat for trout in the southern Appalachians would mean a loss of recreational opportunities and a potential loss of the unique southern Appalachian brook trout strain (SDAFSTC 2005).

Our assumptions about factors affecting trout distribution are unlikely to be realized in a warmer climate. Riparian vegetation, macroinvertebrate food sources, and distributions of other fish will likewise change in response to a warmer climate, but regional-scale impacts of these changes on trout populations are difficult to predict. Changes in land cover, particularly increases in human-dominated land use, are likely to exacerbate habitat loss due to warming.

An increase in water temperature generally causes an increase in metabolism in fish, and the growth rate of trout may either increase or decrease with warming, depending on whether baseline stream temperatures are below or above the optimum temperature, respectively, and the availability of food (Dockray et al. 1996; Jager et al. 1999). In a model based on streams in northern West Virginia, brook trout growth increased with modest temperature increases of 2°C but food became a limiting factor when temperature increases were greater (Ries and Perry 1995). In the southern Appalachians, trout may already be food limited in summer (Whitworth and Strange 1983; Cada et al. 1987; Ensign et al. 1990). In areas like the southern Appalachians, where trout are near the southern margin of their distribution, trout are probably at or near their temperature limits and further increases in temperature could critically increase metabolic costs or exceed thermal limits, resulting in loss of the species from a stream site.

A warmer climate can also change the phenology of organisms. In the southern Appalachians, brook trout are fall spawners and rainbow trout are spring spawners. In a warmer climate, brook trout may spawn later in the fall and hatch earlier due to a warmer winter, and rainbow trout may spawn and hatch earlier in the spring, altering the competitive dynamics between these two species. Furthermore, phenology of food organisms would also change, so that the timing of food availability would no longer be synchronized with that of trout metabolic needs.

Migration is often seen as a coping strategy for plant and animal species, and expected shifts have indeed been detected for some species (Parmesan and Yohe 2003). This strategy is an unlikely solution for trout in the southern Appalachians, where major drainages flow east to the Atlantic Ocean or west and south to the Gulf of Mexico. Geographic constraints of the region limit migration to higher elevations in the same basin, which are already occupied, blocked by barriers, or unsuitable due to lack of reliable flows or stream habitat in very small headwater streams.

Adaptation of trout to warmer temperatures is another coping strategy that may alter the outcome of these models (Rice and Emery 2003). Rapid adaptation to environmental changes, such as a change in thermal regime, is known to occur in fish but the extent to which these processes might occur in this instance is unknown. The high level of fragmentation in a warmer climate and the prevalence of stocked fish from northern environments may limit the ability of populations to adapt to a warmer climate.

Conclusions

Directly modeling the lower elevation boundary of trout distribution in the southern Appalachians with a quantile regression model is a more spatially explicit way to model distribution than previous work that used trout thermal limits. The quantile regression model was independent of any particular limiting temperature for the three species in the trout guild of the southern Appalachians and allowed for other factors to further limit trout habitat in individual streams. Areas with agricultural and human land use are known to be unsuitable for trout, and elimination of these areas resulted in a refined map of trout habitat for the region. Combined with a temperature lapse rate model, the boundary model was the basis for modeling effects of climate warming on trout habitat.

Effects of global climate change could be significant for wild trout in the southern Appalachians, where present-day distributions are already fragmented and restricted to higher elevations. Habitat area and stream length suitable for trout will shrink and become much more fragmented as climate becomes increasingly warm, until only small refuges in headwater streams at the highest elevations will remain. Populations in these small fragments are unlikely to remain viable. Temperature changes, if they happen, will be accompanied by changes in hydrology, riparian vegetation, and land cover patterns that may alter the outcome for trout populations in the southern Appalachians.

Acknowledgments

We thank the coldwater fisheries experts in the southern Appalachians who helped delineate the present-day trout range. We also thank R. Wynne for his assistance with geographical information systems methods, M. Hudy for sharing his data on the additional wild brook trout streams in Virginia and reviewing this paper, and anonymous reviewers for their suggestions. This research was partially funded by the U.S. Forest Service Southern Global Change Program (SRS-4852; S. McNulty). Reference to trade names does not imply endorsement by the U.S. Government.

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