

PREDICTING CLIMATE CHANGE EFFECTS ON APPALACHIAN TROUT: COMBINING GIS AND INDIVIDUAL-BASED MODELING

M. E. CLARK,^{1,4} K. A. ROSE,² D. A. LEVINE,^{3,5} AND W. W. HARGROVE³

¹*Department of Animal Ecology, Iowa State University, Ames, Iowa 50011-3221 USA*

²*Coastal Fisheries Institute and Department of Oceanography and Coastal Sciences,
Louisiana State University, Baton Rouge, Louisiana 70803-7503 USA*

³*Computational Physics and Engineering Division, Oak Ridge National Laboratory,
Oak Ridge, Tennessee 37831-6274 USA*

Abstract. We coupled an individual-based model of brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) with a geographic information system (GIS) database to predict climate change effects on southern Appalachian stream populations. The model tracked individuals of both species through the daily processes of spawning, growth, feeding, mortality, and movement for 30 years in a stream reach consisting of connected pools, runs, and riffles. The southern Appalachian Plateau was divided into 101 watershed elevation band zones. Model simulations were performed for a representative stream reach of each stream order in each zone. Trout abundance was estimated by multiplying predicted trout densities (measured in number of trout per meter) by the total length of streams of each order in each watershed elevation zone. Three climate change scenarios were analyzed: temperature only (1.5–2.5°C warmer stream temperatures); temperature and flow (warmer stream temperatures and lower baseline flows with threefold higher peak flows); and temperature, flow, and mortality episodes (warmer stream temperatures, changed flows, and flow-related scouring of redds). Increased temperature alone resulted in increased abundances of brook and rainbow trout. The temperature-and-flow scenario resulted in a complex mosaic of positive and negative changes in abundances in zones, but little change in total abundance. Addition of episodic mortality in the form of floods that scour redds and kill eggs and fry caused a net loss of rainbow trout. Predicted changes in habitat (based on simulation results and temperature alone) were, at best, weakly correlated with predicted changes in abundance. The coupling of individual-based models to GIS databases, in order to scale up environmental effects on individuals to regional population responses, offers a promising approach for regional assessments.

Key words: brook and rainbow trout; geographic information system (GIS); global climate change; individual-based model; *Oncorhynchus mykiss*; *Salvelinus fontinalis*; southern Appalachian streams; temperature and flow gradients; watershed elevation zones.

INTRODUCTION

The response of aquatic populations to climate change is of considerable importance in determining future species distributions, abundances, and viability (Shuter and Post 1990, Kareiva et al. 1993). The implications of global temperature increases on salmonid populations have been of particular interest (Meisner 1990, Keleher and Rahel 1996). Trout require cold water, and therefore may be especially sensitive to increases in temperature. For instance, Keleher and Rahel (1996) estimated that as much as 38% of current trout stream habitat in Wyoming could be lost with a 3°C increase in July air temperatures.

Trout populations may also be indirectly affected by changes in temperature. Species interactions and competition may be altered as temperature changes (Fausch 1988, DeStaso and Rahel 1994). Flow regimes are likely to undergo substantial changes with increases in global temperatures, because weather patterns, precipitation, and evapotranspiration would be altered (Poff et al. 1996, Mulholland et al. 1997). Flow regimes play a critical role in structuring stream resident trout populations (Onodera and Ueno 1961, Seegrist and Gard 1972). High-flow events can alter community structure through differential mortality and recruitment (Strange et al. 1992), and variation in flow can reduce critical habitat for spawning and fry incubation (Nehring and Anderson 1993). However, studies focusing on changes in trout populations and other cold-water fish species have mostly been limited to simple static analyses of temperature alone to permit large-scale regional assessments (e.g., Meisner 1990, Keleher and Rahel 1996, Rahel et al. 1996).

In this paper, we combine an individual-based simulation model of brook trout (*Salvelinus fontinalis*) and

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⁴ Present address: Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana 59812 USA. E-mail: meclark@selway.umt.edu

⁵ Present address: International Technology Corporation, 312 Directors Drive, Knoxville, Tennessee 37923-4799 USA.

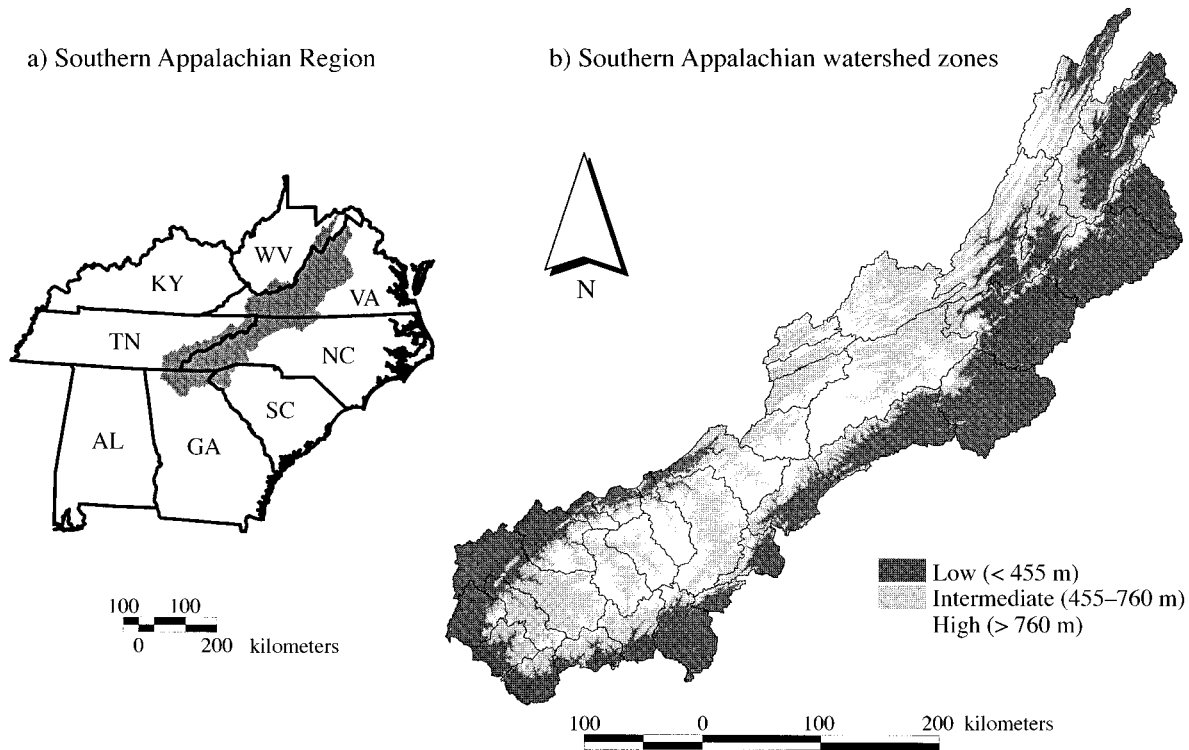


FIG. 1. (a) Region of the southern Appalachians used in model analysis (shaded region), and (b) designated watersheds with elevation zones (low, intermediate, and high) used in compiling environmental data for the spatial components of the trout model.

rainbow trout (*Oncorhynchus mykiss*) with a geographic information system (GIS) database to examine potential responses of Appalachian stream trout populations to global climate change. Brook and rainbow trout in the southern Appalachians offer an interesting case study of climate change effects. Species dominance is regulated by temperature and flow gradients that vary with latitude and elevation across the region (Flebbe 1994, Larson et al. 1995, Clark and Rose 1997a), and temperature and flow are expected to undergo significant changes with increasing atmospheric inputs of CO_2 (Mulholland et al. 1997). Moreover, the individual-based modeling approach permits a detailed and dynamic representation of the biological components of the system (Clark and Rose 1997b). The GIS provides an accurate quantitative means of determining the abiotic components for the simulations, so that the large heterogeneous southern Appalachian region can be modeled. The combination of the individual-based modeling and GIS approaches results in a biologically realistic regional-scale analysis of trout population responses to global climate change.

STUDY REGION

The study region consisted of all streams at elevations >305 m in the southern Appalachian Mountains in the southeastern United States (Fig. 1a). Watershed

characteristics and stream data were assembled into a geographic information system (GIS) database for this region as part of the Southern Appalachian Man and the Biosphere Program (Hermann 1996). Streams at elevations >305 m represent the principal habitat of brook and rainbow trout in the southern Appalachians (Kelly et al. 1980, Flebbe 1994). The study region was divided into watersheds based on U.S. Geological Survey (USGS) hydrologic unit codes. Each watershed was subdivided into three elevation bands (<455 m, $455\text{--}760$ m, and >760 m), which resulted in a total of 101 watershed elevation band zones (Fig. 1b).

Model simulations were performed for a representative stream reach of each stream order (1–6, Strahler method; Allan 1995) present in each of the 101 watershed elevation zones. Trout abundances were estimated by multiplying trout densities (measured in no. trout per meter) by the total length of streams; this was done for each elevation–stream order category. Abundances of each species in each watershed elevation zone were computed by summing abundances over all stream orders in a zone.

MODEL DESCRIPTION

Overview

The brook trout–rainbow trout individual-based population model is briefly described here and is described

in detail in Clark and Rose (1997b). Complete life cycles (egg, alevin, fry, juvenile, and adult stages) of both species are represented in the model. Daily spawning, growth, mortality, and movement of individuals of both species are simulated in streams consisting of sequences of pool, run, and riffle cells. All simulations that we present were for 30 yr. Mean densities of each species were computed using years 5–30 to minimize any effects of initial conditions. We used the same biological components for all simulations, but changed environmental variables to mimic representative streams in each of the 101 watershed elevation zones.

Environmental components

The representative model stream reach was 600 m in total length and consisted of ~150 sequences of pools, runs, and riffle cells. Cells are assigned a length from triangular probability distributions. Minimum, mode, and maximum values define triangular distributions. The modes of the length distributions were 2.0 m for pools, 1.6 m for runs, and 0.4 m for riffles; minimum and maximum values were set to 0.7 and 1.3 times the modal values, respectively. Slopes (in units of meter per meter) were assigned to each pool cell and run cell in a sequence from uniform distributions (pools, 0–0.01; runs, 0.5–1.0). The slope of the riffle cell in each sequence was then determined such that the mean slope over the three cells equaled the specified mean slope of the entire reach.

Temperature, depth, and current velocity were computed daily. Temperature was assumed to be the same for all cells, whereas depth and current velocity were computed from flow and slope. Flow was assumed to be the same for all cells, but depth and current velocity varied among cells on a given day because of the different slopes and geometries of each cell. Clark and Rose (1977b) derived the following computational scheme assuming a power relationship (Richards 1976) between width (w , meters) and depth (d , meters) for each cell ($w = 13.29d^{0.638}$). Maximum depth at the mid-channel (d_{\max}) was computed by first integrating the width-to-depth relationship to determine the cross sectional area for the cell, then setting flow (Q , m³/s) equal to the product of current velocity and the cross sectional area, and finally solving the equation for maximum depth:

$$d_{\max} = 0.105 \left(\frac{Q}{\sqrt{s}} \right)^{3/6.914} \quad (1)$$

where s is the slope of the cell (see Clark and Rose [1997c] for details). Depths at discrete feeding sites within a cell were also computed using the width-to-depth relationship, but with widths corresponding to the distance from the nearest bank to the centroid of each feeding site. Current velocity in each cell (v ; in meters per second) was calculated from Manning's equation (Chow 1959) as follows:

$$v = \frac{1}{n} d_{\max}^{2/3} \sqrt{s} \quad (2)$$

where n is Manning's coefficient (assumed to be 0.045 for small gravel; Chow 1959).

Biological components

Reproduction.—Adult females spawn once per year during the appropriate season (October–December for brook trout, February–April for rainbow trout) in or near their natal cell (Sorenson et al. 1995). Spawning is not allowed in shallow (<10 cm throughout) cells or cells with high velocities (>1 m/s). Fecundity increases with spawner length; for fish of the same length, fecundity is higher for rainbow trout than for brook trout (Lennon 1967, Kelly et al. 1980). Redds are placed randomly in a finer spatial grid within the chosen spawning cell. Brook and rainbow trout are mature at 100 mm in length (Lennon 1967, Larson and Moore 1985, Habera 1987). Eggs and alevins are associated with their redd, develop based on temperature, and experience constant, temperature-based, and habitat-related mortalities. Eggs and alevins can be lost if their redd is scoured by high flows, becomes dry from low flows, or is overcut by a later spawner.

Habitat.—Fry occupy the shoreline margins in cells (defined as water <10 cm deep) away from juveniles and adults, and consume drifting prey that is divided equally among all fry in the cell. Fry are initially located in the same habitat unit as their redd, but may move to shoreline margins in downstream cells due to poor conditions. Transition to the juvenile stage occurs when fry attain 30–40 mm in length. In southern Appalachian streams, young trout are typically >30 mm before entering juvenile and adult habitat (Whitworth and Strange 1983, Habera 1987).

Juveniles and adults prefer to hold and defend feeding sites in the front of pool cells, consuming prey that drifts through the feeding site. Site selection among individual juvenile and adult trout is based on a length hierarchy (Fausch 1984, Hughes and Dill 1990). Fish occupy feeding sites (approximated by fixed 60 × 60 cm squares) in the portion of a cell with depth >10 cm and slope <0.6 m/m (i.e., not in riffles), attacking prey within two body lengths (Grant et al. 1989). Longer fish prevent shorter fish from occupying sites in the same cell. Shorter fish are prevented from using sites adjacent to or upstream of longer individuals within five body lengths of the longer individual. Individuals that are unable to secure a feeding site stay in the back of pools, are the smallest juveniles and adults in the cell, and consume whatever prey are not eaten by those fish with feeding sites. No species-specific differences in competition for feeding sites are incorporated, because previous simulations indicated this had little effect on predicted population dynamics (Clark and Rose 1997a), and evidence supporting such differences for

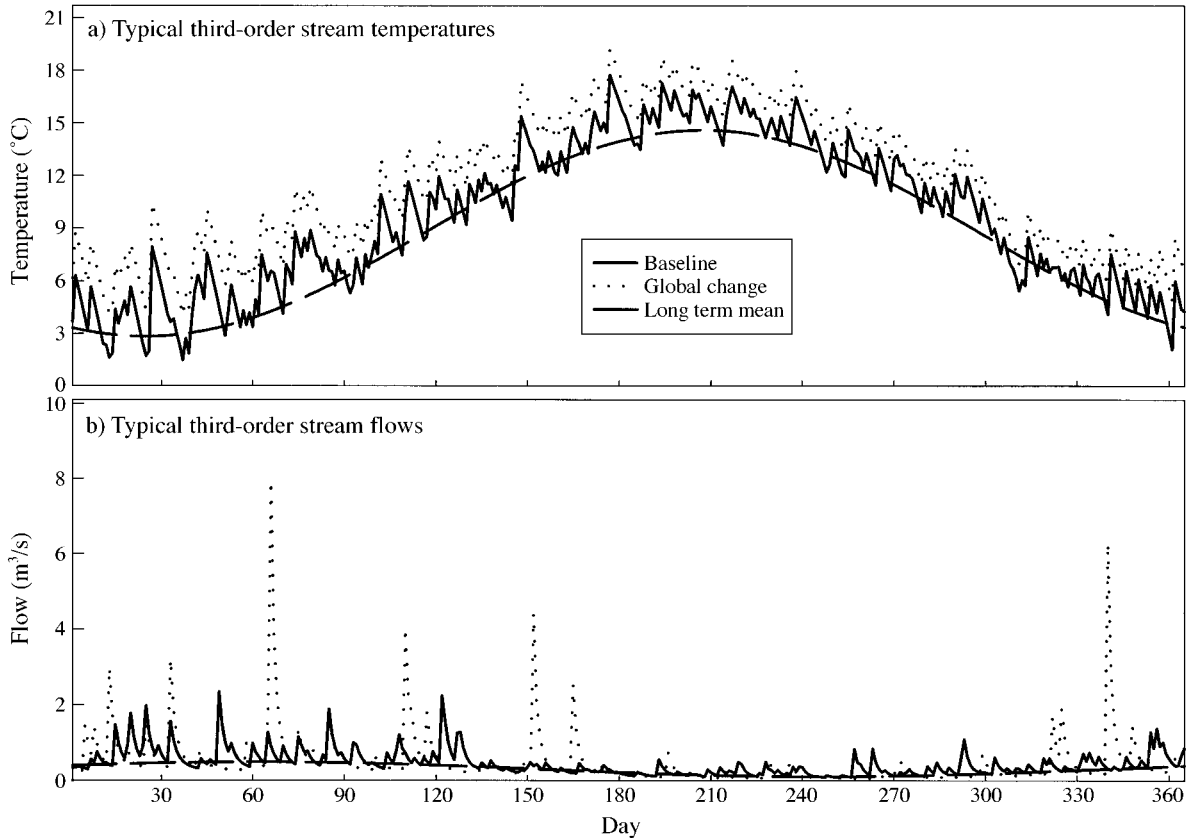


FIG. 2. Stochasticity in (a) temperature and (b) flow, under baseline and global change conditions for a typical third-order stream (at $\sim 35^\circ$ N latitude) model simulation.

brook and rainbow trout in the Appalachians is questionable (Fausch 1988).

Growth.—Growth of fry, juveniles, and adults is based on a bioenergetics model, with consumption and metabolism dependent on fish mass (W , measured in grams wet mass) and water temperature:

$$W_{t+1} = W_t + 0.28pAC_{\max} - 0.19M \quad (3)$$

where C_{\max} is the maximum daily consumption (g wet mass/d), p is the proportion of C_{\max} realized, A is assimilation efficiency, and M is total metabolism (g wet mass/d). Maximum consumption (C_{\max}) is a function of the fish's mass and temperature developed from data reported in Elliott (1975a, b). Assimilation is assumed to be 0.65 for all fish (compared to values of 0.67–0.75 for salmonids reported by Brett and Groves [1979]), because southern Appalachian trout are smaller than similar salmonids in other populations (Carlander 1969, Larson and Moore 1985). Metabolism (M) is a sum of routine (based on mass and a Q_{10} temperature adjustment; Kamler 1992) and active (based on mass swimming speed, and current velocity) components developed for each species, with brook trout metabolism slightly lower than rainbow trout. Optimum temperatures for growth are 9°C for brook trout and 11°C for

rainbow trout (Peterson et al. 1979). Mass is then converted to length on a daily basis, using length–mass relationships developed from data reported in the literature for brook and rainbow trout in the southern Appalachians (see Clark and Rose 1997c).

Calculation of p (the proportion of C_{\max} realized) depends on prey encounters and capture success. Trout are assumed to feed for all daylight hours, except when temperatures are $<2^\circ\text{C}$, when feeding is restricted to one hour per day (Hill and Grossman 1993). A constant invertebrate prey density of $2.7 \text{ mg wet mass/m}^3$ (O'Hop and Wallace 1983, Ensign 1988) is assumed at the front of all cells in the model stream. Prey encounters realized by each trout depend on current velocity at the front of the cell, the cross-sectional area of the feeding site of the individual, and consumption by other trout within the cell. Of the prey encountered, the number subsequently captured and eaten by a trout depends on current velocity and temperature (Hill and Grossman 1993).

Movement.—Fish move from a cell if their growth rate is slow, depths become shallow due to low flow, or current velocity exceeds their maximum swimming speed (Gowan and Fausch 1996, Clark and Rose 1997a, b). Movement is always downstream for fry. For ju-

veniles and adults, direction of movement is random, except when movement is triggered by fast current velocities. During upstream movement, feeding may occur, and swimming costs are incurred. Distance moved is limited to 25 m/d (Whitworth 1980, Gowan and Fausch 1996) by obstruction from an upstream barrier (current velocity greater than maximum swimming speed) or by the upstream and downstream boundaries of the stream.

Mortality.—Mortality of fry, juveniles, and adults is both length and mass-based. Length-based instantaneous mortality rate decreases exponentially from 0.0031 d⁻¹ for a 20-mm trout to 0.0022 d⁻¹ for a 200-mm trout. The length-based relationship was determined from reported apparent (i.e., mortality and emigration combined) mortality rates (McFadden 1961), and to obtain populations dominated by individuals who have attained less than age-3 (Whitworth and Strange 1983) in model simulations. Mass-based mortality occurs when mean mass of an individual falls below a specified percentage (70% for fry; 50% for juveniles and adults) of the mass predicted from the length–mass relationship. For moving fry, an additional 15% daily mortality rate is assumed.

Environment for regional predictions

Representative stream reaches were configured from characteristics of streams in each watershed elevation zone as estimated from the GIS database. Slope, latitude, elevation, and seasonal multipliers of daily temperature were estimated for each zone. Total stream length and seasonal multipliers of daily flow were estimated for each stream order for each zone. All representative streams were configured as 600-m reaches with mean lengths of pools, runs, and riffles from probability distributions as we have described. A single mean slope was used for all representative streams in a watershed elevation zone. Stream slope was set to one-half the estimate of mean slope generated from elevation data in the GIS database. Slopes generated from GIS data were approximately twice the measured slopes of 15 trout streams in the southern Appalachians (Habera 1987), because of the 1-km resolution of the GIS elevation data.

Daily water temperatures were determined specific to each watershed elevation zone, and flows were determined specific to each stream order in each zone. Daily temperatures and flows were determined by adjusting values generated from functions fit to long-term mean values. Both functions were fit to daily values measured during 1977–1982 at a USGS station located on a third-order southern Appalachian stream (station 03497300; Clark and Rose 1997b). Temperatures were adjusted from the function values by multiplying by factors that varied by season (spring, summer, fall, and winter) and by watershed elevation zone. Flows were adjusted by multiplying function values by factors specific to season, zone, and stream order. Stochasticity

was imposed on the long-term mean values by randomly generating runs of above- and below-average temperatures of variable durations and magnitudes, using an algorithm based on a gamma probability distribution (see Clark and Rose [1997b] for details). Typical daily stochasticity in water temperatures and flows are shown in Fig. 2.

Seasonal stream temperature multipliers were calculated from seasonal mean air temperatures computed for each watershed elevation zone. A national network of 4612 meteorological stations was interpolated to assign mean seasonal temperatures to each watershed elevation zone using a spatially and temporally customized adiabatic lapse rate (Hargrove and Luxmoore 1998). Seasonal air temperatures were converted to water temperatures based on a linear regression of measured seasonal air (T_{air} , °C) and stream temperatures (T_{stm} , °C) for two USGS stations (03497300 and 03460000) in southern Appalachian streams ($T_{\text{stm}} = 0.0048 + 0.767T_{\text{air}}$; $r^2 = 0.95$). Winter stream temperatures <4°C were truncated to 4°C for all watershed elevation zones (P. J. Mulholland, *personal communication*). Daily stochasticity could, however, still result in temporary drops below 4°C.

Seasonal flow multipliers were calculated for each stream order in each zone. Multipliers were based on latitude of the zone and the mean watershed area for each stream order in the zone. We first used latitude (lat, °N) to determine mean seasonal flows normalized for watershed area (\hat{Q} , 1000 m³·s⁻¹·ha⁻¹):

$$\hat{Q} = 1.62 + 2.51e^{-1.33(\text{lat}-35.14)} \quad (4)$$

(for spring; $r^2 = 0.60$);

$$\hat{Q} = 0.66 + 2.20e^{-1.28(\text{lat}-35.14)} \quad (5)$$

(for summer; $r^2 = 0.79$);

$$\hat{Q} = 1.00 + 1.74e^{-1.37(\text{lat}-35.14)} \quad (6)$$

(for fall; $r^2 = 0.53$);

$$\hat{Q} = 1.54 + 3.28e^{-0.96(\text{lat}-35.14)} \quad (7)$$

(for winter; $r^2 = 0.61$).

Eqs. 4–7 were estimated from regression analysis of 45 USGS stations. All stations had at ≥10 yr of daily flow measurements, had watershed areas that ranged 4.92–2084.94 km², and were located in 17 of the 36 watersheds (20 of the 101 watershed elevation zones) in the modeled region. Using Eqs. 4–7, we estimated the seasonal normalized flows for each watershed elevation zone based on the GIS estimate of the latitude of the center of each zone. Mean seasonal flow (in units of cubic meters per second) was then computed for each order stream in each zone by multiplying the normalized flow by the mean watershed area associated with that stream order.

Computation of mean watershed area by stream order in each zone was performed with the GIS. Requiring

watershed areas for each elevation band in a zone complicated calculations, because streams in higher elevation bands can contribute to the watershed area of lower order streams in contiguous lower elevation bands. Mean watershed area of stream order i in a particular watershed elevation zone is given by the following:

$$\bar{A}_{\text{zone},i} = \frac{l_{\text{zone},i}}{\sum_{j=1}^6 l_{\text{zone},j}} \left(\frac{\text{TA}_{\text{zone}}}{n_{\text{zone},i}} \right) + \frac{\bar{A}_{\text{zone above},i} \times \gamma_{\text{zone above},i}}{n_{\text{zone},i}} + \sum_{j=1}^{i-1} \frac{(n_{\text{zone},i-j} - \gamma_{\text{zone},i-j}) \bar{A}_{\text{zone},i-j}}{\sum_{k=1}^6 n_{\text{zone},k} - \sum_{k=1}^{i-j} n_{\text{zone},k}} \quad (8)$$

where “zone” corresponds to the low, intermediate, or high elevation zone of the watershed, $l_{\text{zone},i}$ is the total length of streams of order i in the watershed elevation zone, TA_{zone} is total area of the watershed elevation zone, $n_{\text{zone},i}$ is the number of streams of order i in the watershed elevation zone, and $\gamma_{\text{zone},i}$ is the number of streams of order i exiting the watershed elevation zone.

The three terms of Eq. 8 have the following interpretations. The first term is the mean watershed area of streams of order i in the zone. We use the ratio of the total length of streams of order i to the total length of all streams to partition the total area of the zone to the area contributing to order i streams; we divide by the total number of streams of order i to convert total area to mean area per stream. The second term accounts for streams of order i that enter the zone from the next higher elevation band. The mean area for a stream in the next higher elevation band is converted to a total area by multiplying by the number of streams of order i that exit the next higher elevation band. This total area is then divided by the total number of streams of order i in the zone of interest, in order to convert total area to an mean area per stream. The third term accounts for streams of lower order than i that terminated in the zone of interest. Streams of lower order than i that terminated must have drained into higher order streams. The summation is over all streams of less than the i th order. For each stream of lower order j , total area of order j streams, shown in the numerator, is the product of the mean area for an order j stream and the difference between the number of order j streams in the zone and the number of order j streams that exit the zone. The total area of order j streams is divided by the total number of streams with orders higher than j , which is the difference between the total number of streams in the zone and the total number of order j and lower streams (shown in the denominator). This is the mean area contributed by lower order streams per higher order stream in the zone.

Model corroboration and dynamics

Model corroboration consisted of comparing predicted trout densities and growth rates from the 600-

m representative stream reach (third-order at 35° N latitude) to data from sympatric populations in southern Appalachian streams (Clark and Rose 1997b). We reproduce some of the corroboration results here. Three replicate 100-yr simulations were performed. The mean stream slope was set to 0.1 m/m (Moore et al. 1983, Larson and Moore 1985), and daily temperatures and flows were based on long-term mean values with stochasticity imposed (Fig. 2).

Predicted brook and rainbow trout coexisted at realistic densities that were negatively correlated (Fig. 3). Predicted annual densities (averaged over all days of the year) were similar in magnitude to those reported for southern Appalachian streams. Predicted annual densities were ~0.10 brook trout/m² (compared to reported densities of 0.02–0.22 trout/m²) and ~0.13 rainbow trout/m² (compared to 0.02–0.18 trout/m²) (Larson and Moore 1985, Ensign et al. 1991). Mean annual rainbow trout densities were ~1.3-fold higher than brook trout densities and were negatively correlated to brook trout densities ($r^2 = 0.44, 0.33, \text{ and } 0.27$ for the three replicate simulations, respectively). Predicted growth rates and lengths were also similar to values reported in the literature for trout in southern Appalachian streams (Table 1). Density dependence was strongest in the fry stage, with fry growth rates each year negatively related to initial fry densities for both species (mean r^2 across replicates of 0.28 for brook trout and 0.53 for rainbow trout). Fry survival was positively correlated to growth rate ($r^2 = 0.42$ for brook trout and 0.62 for rainbow trout).

REGIONAL SIMULATIONS UNDER CLIMATE CHANGE

Scenarios

Three climate change scenarios were analyzed: temperature only; temperature and flow; and temperature, flow, and episodes of high mortality. The temperature-only scenario involved increasing temperatures above baseline levels. The temperature-and-flow scenario involved increasing temperature as in the temperature scenario, but also included higher magnitude, but less frequent, high-flow events. The third scenario added a current velocity-based mortality to redd survival, resulting in episodic losses of redds due to high-flow events. The first two scenarios were performed under sympatric conditions (both species present initially); the temperature, flow, and episodes scenario was performed under sympatric and allopatric (brook trout only and rainbow trout only) conditions.

Analysis of the three scenarios required nine sets of simulations of the 101 watershed elevation zones (Table 2). Each set involved 404 model simulations to cover all of the stream orders found in each of the 101 watershed elevation zones. The first three sets of simulations were baseline, the temperature-only scenario, and temperature-and-flow scenario, all under sympatric conditions. The next six sets of simulations included

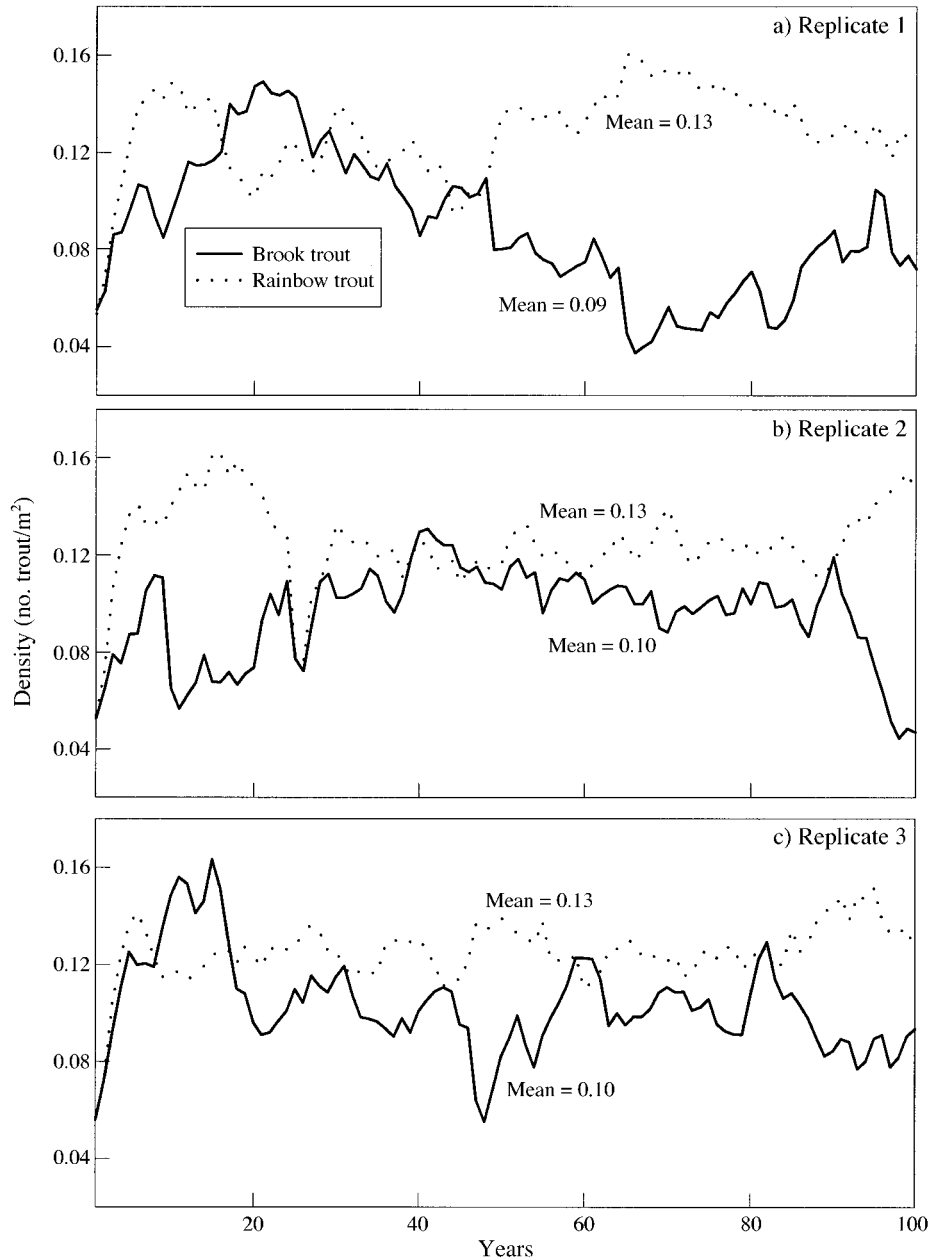


FIG. 3. Predicted annual brook and rainbow trout postfry densities for three replicate (sympatric) simulations of a typical third-order, 35° N latitude southern Appalachian trout stream.

current velocity-based redd mortality (episodes). Baseline and the temperature, flow, and episodes scenario were simulated under sympatric and allopatric conditions. The baseline set of simulations was the same for the temperature-only and temperature-and-flow scenarios. There were three different baseline sets of simulations for current velocity-based redd mortality: sympatric, brook trout only, and rainbow trout only. Predicted trout abundances under the three scenarios were always compared to their respective baseline values.

We included the temperature-only scenario, because

most climate change assessments on fish focus on the effects of increased temperature (e.g., Meisner 1990, Keleher and Rahel 1996). The temperature-and-flow scenario corresponded to the current thinking concerning the major hydrological changes expected for streams in the southeastern United States under climate change (Mulholland et al. 1997). We added the current velocity threshold to redd survival, because episodic high mortality of redds linked to flow events is an important feature of trout population dynamics in southern Appalachian streams (Lennon 1967, Kelly et

TABLE 1. Mean values of life-stage-specific duration, survival, growth rate, and mean length from three replicate, 100-yr duration simulations of the brook trout-rainbow trout model configured for a 35° N, southern Appalachian stream with sympatric populations (from Clark and Rose 1997a).

Life stage	Stage duration (d)	Survival (fraction)	Daily growth rate (g/g)		Mean length (mm)	
			Predicted	Observed	Predicted	Observed
Brook trout						
Eggs and alevins	158	0.13
Fry	33	0.19	0.05	0.06†	31‡	...
Juveniles (<100 mm)	137	0.68	0.027	...	100§	...
Age 1	251	0.52	0.016	0.006	116	86, 101,¶ 149#
Age 2	365	0.44	0.003	0.004	164	139, 136,¶ 174#
Age 3	365	0.45	0.001	0.0006	185	155, 160,¶ 196#
Rainbow trout						
Eggs and alevins	69	0.12
Fry	41	0.10	0.04	0.04†	31‡	...
Juveniles (<100 mm)	173	0.63	0.021	...	100§	...
Age 1	312	0.45	0.013	0.009	115	104, 131††
Age 2	365	0.43	0.003	0.005	164	180, 170††
Age 3	365	0.44	0.001	0.0002	186	185, 208††

† Rose (1986).

‡ Length at end of fry stage.

§ Length at maturity.

|| Whitworth (1980).

¶ Konopacky and Estes (1986).

Lennon (1961).

†† Lennon and Parker (1959).

al. 1980). Previous model simulations showed year-class failures to be an important determinant of species dominance (Clark and Rose 1997a), and the frequency of such events may increase under climate change. Allopatric conditions were included in the temperature, flow, and episodes scenario to determine the robustness of model predictions under sympatry. All streams initially assumed to be sympatric, or all streams initially assumed to be allopatric, represent the extreme situations; the southern Appalachians contain a mix of sympatric and allopatric streams (Kelly et al. 1980, Flebbe 1994).

Temperature changes used for all three scenarios consisted of increasing daily temperatures in the spring

by 2.0°C, in the summer and fall by 1.5°C, and in the winter by 2.5°C (e.g., Fig. 2a). These increases were based on recent predictions of general circulation models for conditions in the southeastern United States under a doubling of current CO₂ levels (Mulholland et al. 1997).

Flow changes under climate change consisted of less frequent, but higher magnitude, high-flow events (e.g., Fig. 2b). Regional climate models predict more extreme hydrographs with higher peak flows, but lower base flows (especially in summer), for streams in the southeastern United States under increased atmospheric CO₂ conditions (Mulholland et al. 1997). We increased the magnitude of high-flow events approximately three-

TABLE 2. The nine sets of simulations of the 101 watershed elevation zones used to compare the three climate change scenarios to baseline conditions.

Simulation	Scenario	Initial species composition			Increased temperature	Altered flow	Velocity-based redd mortality
		Sympatric	Brook only	Rainbow only			
1	B	X					
2	T	X			X		
3	T, F	X			X	X	
4	B	X				X	
5	T, F, E	X			X	X	
6	B		X			X	
7	T, F, E		X		X	X	
8	B			X		X	
9	T, F, E			X	X	X	

Notes: Each set involved 404 model simulations for a grand total of 9696 model simulations used in the analysis. The three scenarios are abbreviated as follows: B = baseline; T = temperature only; T, F = temperature and flow; and T, F, E = temperature, flow, and episodes.

fold above baseline, but imposed them at approximately one-half the frequency as under baseline (P. J. Mulholland, *personal communication*). The reduced frequency of high-flow events in summer resulted in lower mean summer flows under climate change, compared to baseline.

Current velocity-based redd mortality consisted of killing all eggs and alevins whenever daily current velocity exceeded 0.55 m/s in the cell. More than 99% of redds are located in pools. The 0.55 m/s threshold current velocity was selected because it represents a very high velocity for pool habitat (>95% of all pools had velocities <0.55 m/s in most third-order model streams under baseline), but occurred frequently enough to result in near year-class failures (>50% redd loss) on an ~10-yr basis. Redd destruction associated with high-flow storm events is an important factor affecting southern Appalachian trout streams (Harshbarger 1975). Empirical evidence for current velocity-related redd destruction does not exist, but previous model simulations indicated year-class failures occurring on an ≤ 10 -yr basis may contribute to numerical dominance of rainbow trout over brook trout in southern latitude streams of the Appalachians (Clark and Rose 1997a).

Prediction variables

Brook and rainbow trout abundances were computed from predicted mean densities and stream lengths. Mean densities of each species (measured in no. individuals per meter) were computed using years 5–30 of each simulation of each order in each of the 101 watershed elevation zones. Trout abundances per stream order in each zone were calculated by multiplying the predicted densities per meter of representative stream by the total length of that order stream (measured in meters) in the zone. Abundances were summed over all stream orders and watershed elevation zones to yield total abundance in the Southern Appalachians, and summed by stream order, elevation band, and latitude class (midpoints of 34, 35, 36, 37, 38, and 39°N).

Two habitat measures were computed for comparison; the first (model-based habitat) was based on the total lengths of streams that were predicted to have persistent populations in simulations, while the second (temperature-based habitat) was based solely on mean summer water temperatures. For model-based habitat, persistence was defined as mean densities (computed over years 5–30) >0.005 trout/m. In previous simulations, populations with mean densities below ~0.006 trout/m went extinct within 100 yr (Clark and Rose 1997a). Habitat supporting viable populations was determined for each species as the total lengths of streams of each order with persistent populations of that species. Habitat was expressed as no. kilometers per zone (summed over orders) and total (summed over orders and zones). Temperature-based habitat was included for

comparison to previous climate change analyses, which relied strictly on static analysis of stream temperature. Temperature-based habitat was defined as the total length of streams (km) with mean summer water temperatures <19°C. Eaton et al. (1995) estimated brook and rainbow trout thermal tolerance limits at 22°C and 24°C, respectively. The 19°C threshold was selected because, in model simulations, maximum summer temperatures (lasting three to four days) are ~3°C higher than the mean summer temperature.

Predicted abundances and habitat are reported as both absolute amounts and changes from baseline values, with abundances expressed as no. trout. Changes are computed as the relative percentage change from baseline [$100 \cdot (y - y_B) / y_B$], where y is the mean value under climate change and y_B is the mean value under baseline conditions.

We first present results showing the major effects of climate change on brook and rainbow trout abundances. We compare baseline and the three climate change scenarios performed under sympatric conditions. We present maps of predicted changes in abundances by zone, between baseline and each of the three climate change scenarios. Next, mean values of annual egg production, number of spawners, stage-specific survival rates, and summertime growth rates of fry and adults are compared across representative simulations to help explain model responses. We report mean values computed using 45 randomly selected watershed elevation zones. Outputting the necessary data from all simulations increased computation time excessively, while mean values from the 45 randomly selected zones differed from values based on all zones by <5%. Finally, total abundances, and abundances by stream order, elevation band, and latitude class, are compared between baseline and the three scenarios.

The second grouping of results examines the robustness of model predictions to the assumption in model simulations of sympatric initial conditions in all streams. We use the sympatric and allopatric simulations performed under the temperature, flow, and episodes scenario (compared against baseline in sympatry and baseline in allopatry; Table 2). The changes from baseline in total and elevation band-specific abundance, and in total and elevation-band specific model-based habitat, are compared for brook and rainbow trout in simulations started with all streams sympatric and with all allopatric. Similar predicted changes in abundance and habitat under sympatry and allopatry would imply that model predictions were robust to the assumption of sympatric initial conditions.

The third grouping of results involves comparison of predicted changes in abundance with predicted changes in the two measures of trout habitat. We compare predicted abundance, model-based habitat, and temperature-based habitat between the baseline and the temperature, flow, and episodes scenario (under sympatric initial conditions). We show scatter plots of the

predicted relative changes in model-based habitat vs. predicted changes in abundances, as well as in predicted changes in model-based habitat vs. predicted changes in temperature-based habitat for each of the 101 watershed elevation zones.

Simulation details

We performed a single 30-yr simulation for each stream order in each watershed elevation zone. The individual-based model is stochastic. We generated a unique stream morphology (slope; pool, run, and riffle lengths) for each stream order and zone, but then used the same stream morphology for all scenarios. Similarly, we generated stochasticity in daily temperature as deviations from seasonally adjusted values that were unique for each stream order and zone, but then used the identical climate series for each order and zone across all scenarios. Under climate change scenarios, the deviations were imposed on the increased temperature values. Stochasticity in flow was done in the same way as stream morphology and temperature; unique deviations for each stream order and zone were maintained across scenarios. The only difference was that two sets of deviations were needed, corresponding to scenarios without and with climate-altered flow.

Initial conditions were the same for all simulations: 100 male and 100 female individuals of both species (sympatric) or of each species (allopatric) with initial lengths randomly assigned as 55–57 mm. We used predicted mean trout densities from a single simulation; predicted mean densities from replicate simulations with different morphologies and different temperature and flow stochasticity differed by <10%.

RESULTS

Abundance

Predicted changes in trout abundances differed among climate change scenarios (Figs. 4 and 5). Increased temperature alone resulted in increased abundances of brook and rainbow trout throughout almost all of the zones; total abundance increased by 4.6×10^6 (77%) for brook trout and 3.0×10^6 (26%) for rainbow trout (Fig. 5). Increased temperature and flow together resulted in a complex mosaic of positive and negative changes in trout abundances, when viewed on a zone-by-zone basis, but in little change in the total abundance of either species. Addition of episodic mortality to temperature and flow changes also caused a wide range of zone-specific changes in abundances, with a net loss of rainbow trout and little change in brook trout total abundance. Even under the greatest predicted negative change in trout abundance (rainbow trout under the temperature, flow, and episodes scenario), several zones showed increases in abundance >500%.

Changes in temperature and flow affected spawning success and the survival of early life stages (Table 3).

Under increased temperature alone, warmer spring temperatures increased the development rates of eggs, which, with constant mortality rates, resulted in increased survival (brook trout ~0.3–0.4; rainbow trout, ~0.16–0.23). Fry growth was density dependent, and higher egg survival led to more fry, slower fry growth rates, and lower fry survival. Survival and growth of other life stages were similar between baseline and the increased temperature only scenario. Increased egg survival offset the lower fry survival, and the number of spawners and annual egg production increased under increased temperature for both species.

Changing temperature and flow also resulted in increased egg survival and lower fry survival, but affected rainbow trout more than brook trout (Table 3). The higher peak flows under climate change (Fig. 2) occurred when rainbow trout spawn (January–March) and disrupted spawner movement and eliminated suitable spawning areas. Lowered spawning success offset increased egg survival, and the number of spawners and annual egg production of rainbow trout decreased under the temperature-and-flow climate change scenario (Table 3). The effect of flow on spawning success was not as strong for brook trout, because peak flows under climate change were not as high during their fall spawning season (Fig. 2) and did not disrupt spawner movements (effects of flow on redd success were not included in this scenario). The number of spawners and annual egg production of brook trout were similar between baseline and the increased-temperature and altered-flow climate change scenario.

Adding a current velocity-related mortality to temperature and flow changes negated the temperature-induced increase in egg survival (Table 3). Egg survival was similar between baseline and the temperature, flow, and episodes scenario for both species. Alevin and fry survival of rainbow trout was lower under this climate change scenario, due to scouring from high flows. However, brook trout alevin survival increased because higher flows reduced dewatering losses (but were not high enough for scouring) and fewer rainbow trout spawners reduced overcutting losses. With the increase in egg survival from increased temperatures offset by increased redd mortality, due to higher velocities, the number of spawners and level of egg production were dramatically reduced under the temperature, flow, and episodes scenario for both brook and rainbow trout.

Predicted changes in abundances depended on stream order, elevation band, and latitude for the temperature, flow, and episodes scenario only. The temperature-only scenario caused increased brook and rainbow trout abundances across all stream orders, for all three elevation bands, and across all six latitude classes (Fig. 6a, b). Temperature and flow together, which resulted in little net change in total trout abundances for the region (Fig. 5), also showed little changes across order, elevation, and latitude (Fig. 6c, d). The response of rainbow trout under temperature, flow, and

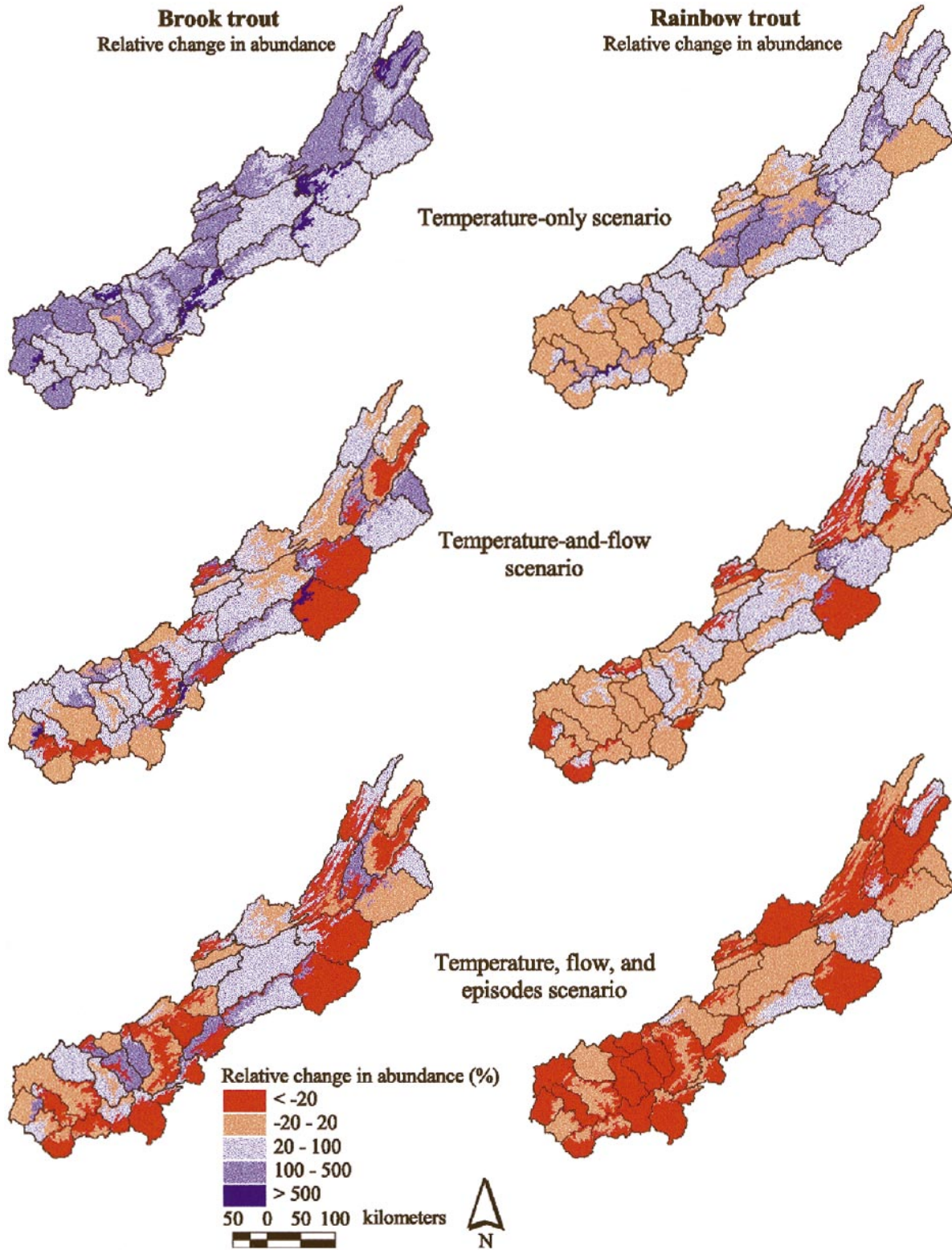


FIG. 4. Relative change in predicted trout abundance in each of the watershed elevation zones (outlined in black), between sympatric baseline and each of the three global climate change scenarios for brook trout and rainbow trout.

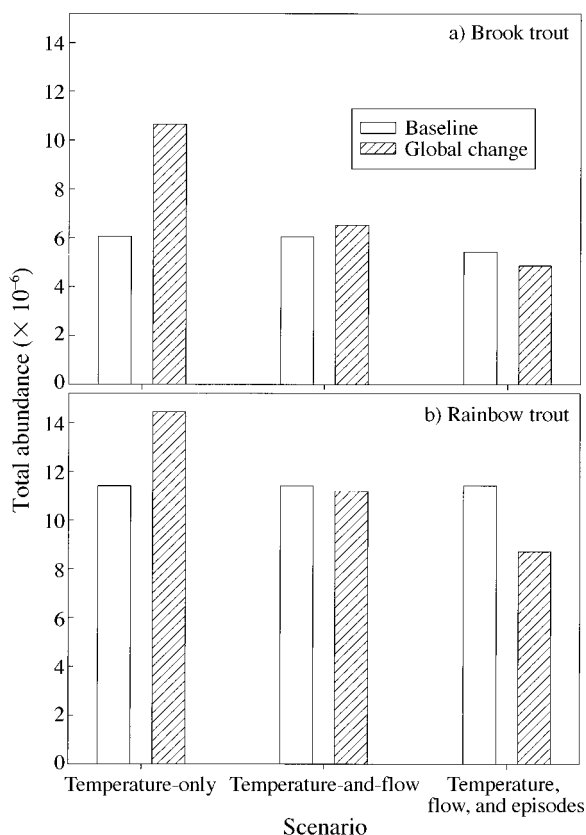


FIG. 5. Predicted abundances of (a) brook trout and (b) rainbow trout for the temperature-only, temperature-and-flow, and temperature, flow, and episodes climate change scenarios. All simulations used sympatric initial conditions. Abundance is measured in millions of fish.

episodes scenario varied with order, elevation, and latitude. Predicted reductions increased with decreasing elevation, increasing stream order, and decreasing latitude (Fig. 6f). The greatest reductions in rainbow trout abundances occurred in large, low-elevation streams located at the southern end of the region. Higher order streams have higher peak flows (and therefore higher

peak velocities) that killed greater numbers of eggs and alevins. Stream order and elevation are roughly correlated, as larger streams tend to be found at lower elevations. Flows were highest in the southern end of the modeled region. Predicted changes in brook trout (Fig. 6e) also tended to show a similar pattern as rainbow trout, but with smaller magnitudes of changes that made the patterns with brook trout less obvious.

Sympatry vs. allopatry

Predicted effects of climate change were generally insensitive to the assumption of sympatric or allopatric initial conditions. Greater reductions in total abundances were predicted for both species under allopatry than sympatry, while the magnitude of model-based habitat losses were similar under allopatry and sympatry. Brook trout abundance decreased 10% in the temperature, flow, and episodes simulation from baseline when the initial species composition in streams included both brook and rainbow trout (i.e., in sympatry; Table 2). However, brook trout abundance decreased 28% when the initial species composition only included brook trout (i.e., in allopatry; Table 2 for both baseline and temperature, flow, and episodes). Similarly, rainbow trout abundance decreased 24% (from baseline in the temperature, flow, and episodes simulation) in sympatry, compared to 38% in allopatry. Brook trout habitat loss went from 24% under sympatry to 27% under allopatry, while rainbow trout habitat loss went from 16% to 22%.

Predicted changes in model-based habitat and abundance by elevation also were consistent between sympatry and allopatry, except for brook trout abundance in high elevations. Brook trout abundance increased by 25% under sympatry, but decreased by 30% under allopatry, for streams with elevations >760 m. While these percentage changes are large, they involve relatively few fish. Fewer than 10% of the total abundance of brook trout were found in these high-elevation streams.

TABLE 3. Mean egg production (per 600-m stream reach), no. spawners (per 600-m stream reach), life-stage-specific survival (fraction), and growth (mm/d) of brook and rainbow trout from 45 of the 404 simulations for baseline (B) and global change (G) conditions for the temperature-only (T), temperature-and-flow (T, F), and the temperature, flow, and episodes (T, F, E) scenarios.

Scenario	No. eggs/yr		No. spawners/yr		Survival (fraction)								Growth (mm/d)			
					Eggs		Alevins		Fry		Adults		Fry		Adults	
	B	G	B	G	B	G	B	G	B	G	B	G	B	G	B	G
Brook trout																
T	13 480	23 640	71	112	0.30	0.41	0.40	0.42	0.23	0.16	0.47	0.46	0.39	0.36	0.18	0.17
T, F	13 480	14 742	71	70	0.30	0.35	0.40	0.42	0.23	0.19	0.47	0.45	0.39	0.39	0.18	0.15
T, F, E	8 723	3 346	49	21	0.27	0.25	0.38	0.46	0.22	0.18	0.45	0.36	0.38	0.32	0.16	0.08
Rainbow trout																
T	61 556	82 287	132	156	0.16	0.23	0.72	0.74	0.12	0.07	0.44	0.45	0.31	0.29	0.22	0.22
T, F	61 556	56 351	132	108	0.16	0.21	0.72	0.72	0.12	0.08	0.44	0.42	0.31	0.31	0.22	0.20
T, F, E	56 387	19 469	123	49	0.15	0.15	0.70	0.60	0.13	0.09	0.43	0.39	0.31	0.31	0.21	0.15

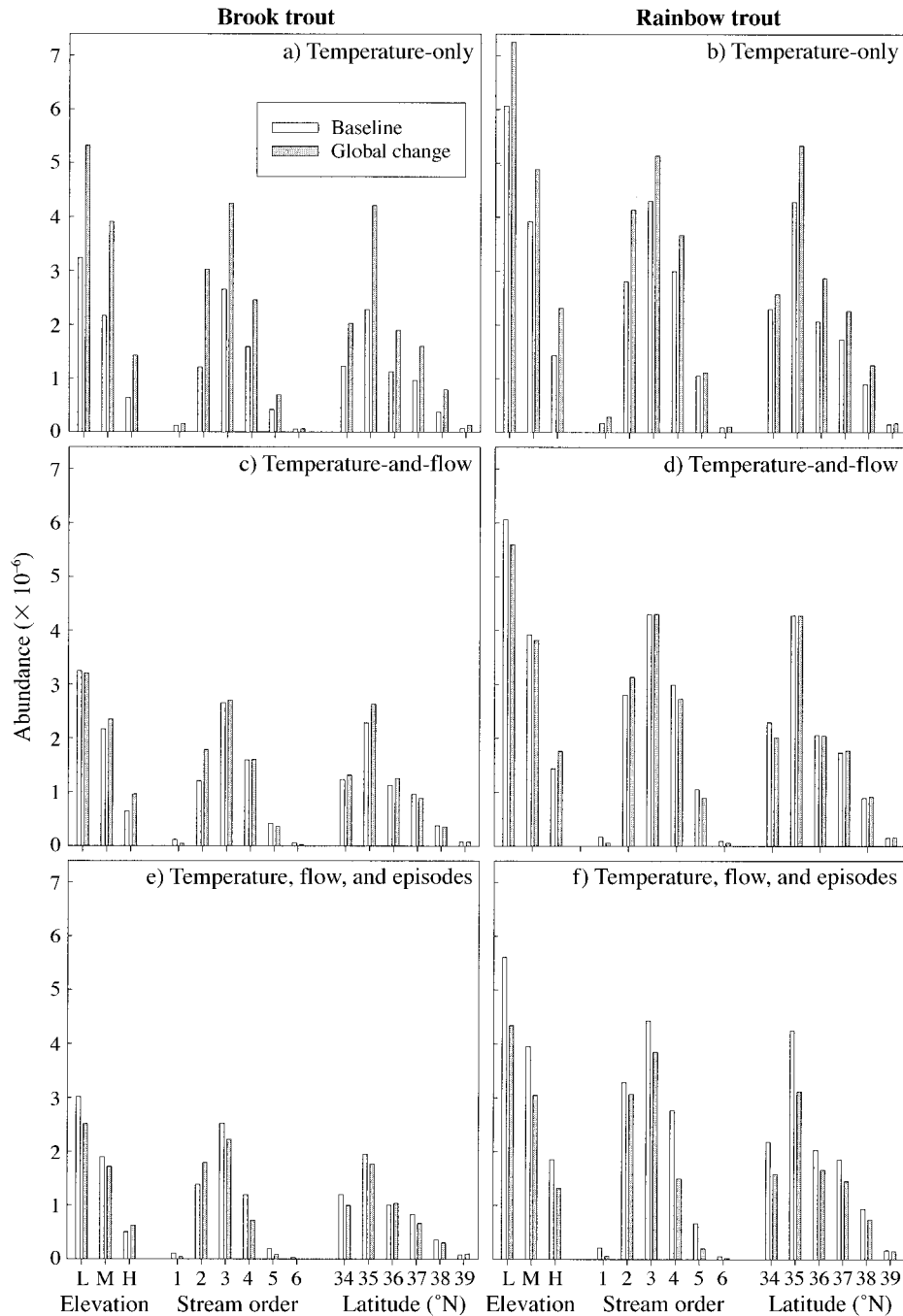


FIG. 6. Predicted abundances of brook trout and rainbow trout across elevation bands (L, <455 m; M, 455–760 m; H, >760 m), stream orders, and latitude for the (a and b) temperature-only scenario, (c and d) temperature-and-flow scenario, and (e and f) the temperature, flow, and episodes scenario. All simulations used sympatric initial conditions. Abundance is measured in millions of fish.

Habitat changes

Changes in total model-based habitat were more similar to changes in abundances than they were to changes in temperature-based habitat (Table 4). Changes in model-based habitat, which used predicted densities to determine persistence, were of similar magnitude to

those based on abundances. Model-based habitat showed a 24% loss of brook trout habitat, compared to a 10% reduction in abundance, and a 16% loss in rainbow trout habitat, compared to a 24% reduction in abundance. In contrast, temperature-based habitat showed an 80% reduction. A single value is predicted,

TABLE 4. Predicted total abundances, model-based habitat, and temperature-based habitat for the baseline and the temperature, flow, and episodes climate change scenarios, with percentage change between climate change and baseline also shown.

Variable	Brook trout			Rainbow trout		
	Baseline	Climate change	Change (%)	Baseline	Climate change	Change (%)
Abundance ($\times 10^{-6}$)	5.417	4.857	-10	11.408	8.702	-24
Model-based habitat (km)	25 032	19 069	-24	27 391	23 015	-16
Temperature-based habitat (km)	63 484	12 749	-80	63 484	12 749	-80

Note: Temperature-based habitat is the same for brook and rainbow trout, because it is based only on the total length of streams with summer temperatures $<19^{\circ}\text{C}$.

because the 19°C maximum was used for both trout species.

When compared on a zone-by-zone basis, predicted changes in model-based habitat were only weakly correlated with predicted changes in abundances and were uncorrelated with predicted changes in temperature-based habitat (Fig. 7). Values of the change in temperature-based habitat, compared to baseline, were either zero (no change) or -100% (habitable in baseline to uninhabitable) for each zone. Model-based habitat and abundances were continuous variables. Changes in model-based habitat and abundances were weakly correlated (brook trout, $r^2 = 0.07$; rainbow trout, $r^2 = 0.45$). Brook trout had low r^2 because of scatter and

many 0% habitat changes being associated with non-zero changes in abundance. Model-based and temperature-based habitat changes showed little consistency across zones.

DISCUSSION

We performed a regional-scale analysis of climate change effects using a detailed, individual-based simulation model of brook and rainbow trout population dynamics. Changes in temperature and flow were scaled up from individual organism responses to the regional level. Previous studies of regional responses of coldwater fishes to climate change have relied on static analyses that use thermal stress limits to deter-

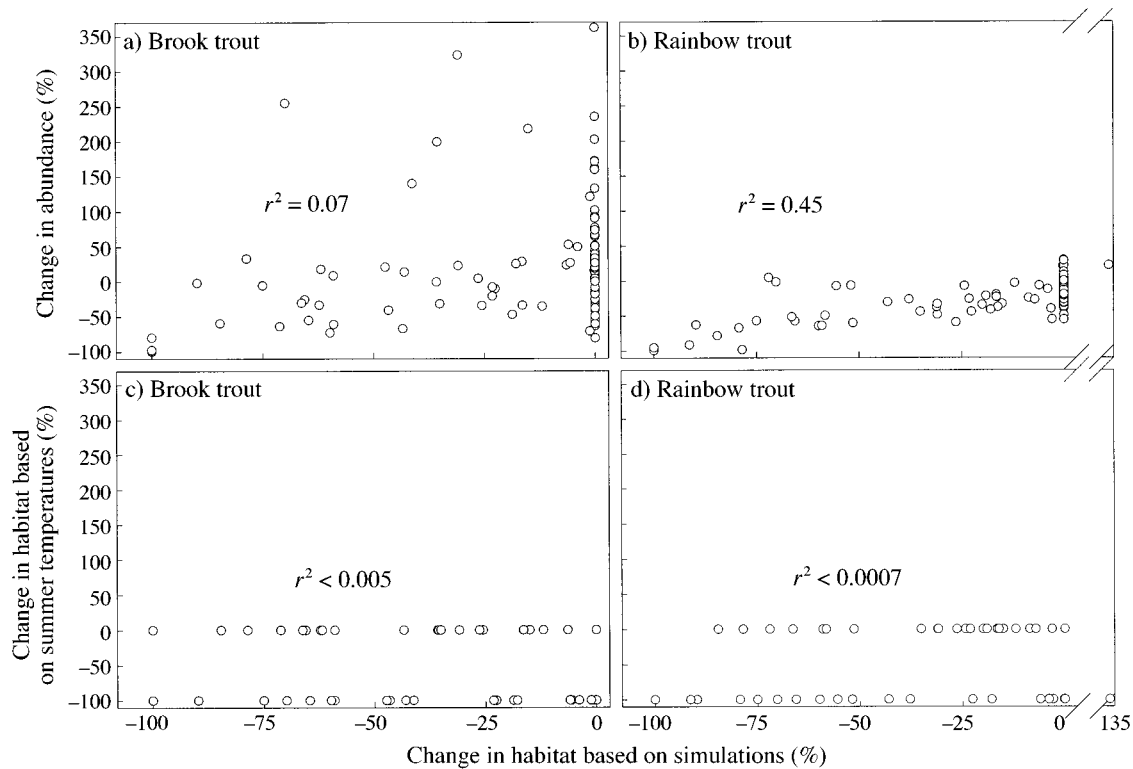


FIG. 7. Correlation (a and b) between predicted changes in abundance and changes in model-based habitat, and (c and d) between predicted changes in temperature-based habitat and changes in model-based habitat, for brook and rainbow trout. All predicted changes are based on the difference between the baseline simulation and the temperature, flow, and episodes climate change scenario, both using sympatric initial conditions.

mine changes in potential trout habitat (Meisner 1990, Keleher and Rahel 1996). Our approach allowed for dynamic simulation of trout populations, including their spawning, growth, survival, and movement, and the responses of these processes to climate change-induced alterations in daily temperature and flow.

Marschall and Crowder (1996) used an age-structured model to show that early life stages were the most critical periods for southern Appalachian brook trout. Competition with rainbow trout as young juveniles and changes in egg survival had larger effects on the population size of brook trout than changes in their adult mortality. The individual-based model used here demonstrates comparatively similar behavior (Clark and Rose 1997a, c). Factors affecting egg and fry survival have the greatest impact on the population dynamics (and competitive dominance). Hence, in the temperature-only scenario, warmer temperatures reduced egg and alevin development time, egg-to-fry survival increased, and trout populations increased. However, the spatially explicit form of our model permitted the incorporation of other factors, primarily flow related, that can affect individuals during their early life stages.

Our results demonstrate the importance of considering flow-related effects when predicting trout population responses to climate change. Including flow changes with temperature changes negated the increases in trout abundances predicted under a temperature-only scenario, and adding a current velocity-based mortality relationship resulted in net loss of rainbow trout (Fig. 5). Predicting effects of episodic mortality events is very difficult without a spatially explicit numerical model of spawning, growth, survival, and movement. Changes in flow appear to be as important, or more important, than changes in temperature for predicting trout responses to climate change in southern Appalachian streams.

Predicted changes in habitat are not necessarily the same as changes in abundance. Based on a statistical model of groundwater, Meisner (1990) projected losses of brook trout habitat of 40–50% in the southern Appalachian region (visually estimated from Meisner [1990: Fig. 3]). Our temperature-based habitat also showed a large reduction (80%) in trout habitat under the 1.5–2.5°C increases. The same 80% loss would be predicted for both species for all three scenarios, because habitat was based only on temperature, which was changed in the same manner for all scenarios. Yet, under our temperature-only scenario, the individual-based model predicted net increases in brook and rainbow trout abundances (Fig. 5). Furthermore, under the realistic temperature, flow, and episodes scenario, predicted reductions in total abundance were 10% for brook trout and 24% for rainbow trout, much less than the 80% predicted using temperature-based habitat. Finally, predicted changes in temperature-based habitat showed little correspondence with predicted changes in model-based habitat or abundance on a zone-by-zone

basis (Fig. 7). Predictions of abundances result from a complex set of negative and positive effects of increased temperature and altered flow on spawning, growth, mortality, and movement.

Predicted changes in habitat were more similar to changes in abundance when model-predicted densities were used to define habitat, but even this did not result in agreement on a zone-by-zone basis. Our designation of streams as supporting or not supporting persistent populations, based on predicted mean trout densities, was analogous to a presence–absence classification. Predicted changes in model-based habitat were only weakly related to changes in abundances when viewed on a zone-by-zone basis (Fig. 7). Reducing the information to presence–absence distorted predictions of climate change effects, even when the presence–absence designation was based on predicted densities. Model-based habitat and abundances were more similar on a regional scale; both predicted reductions of 10–25% (Table 4). Expressing climate change effects as changes in habitat can be useful as a first approximation to how spatial distributions (presence–absence) may change under climate change, but should not be confused with abundance.

Model simulations did show significant effects of climate change on trout populations in the southern Appalachians. We consider the temperature, flow, and episodes scenario as the most realistic simulation of climate change effects. Under this scenario, model-based habitat was predicted to decline by 24% for brook trout and by 16% for rainbow trout (Table 4). In terms of abundance, we predicted a net decrease of 10% in brook trout and of 24% in rainbow trout (Table 4), and a complicated spatial redistribution of both species. Predicted positive and negative changes in abundances showed a complex mosaic among the 101 watershed elevation zones for both species, with most zones showing small losses (~20%) and a few showing dramatic increases (Fig. 4). There was a suggestion that effects were greatest in low-elevation southern streams. Predicted reductions in rainbow trout, and to a lesser extent in brook trout, were greatest in large, low-elevation streams located at the southern end of the region (Fig. 6). Low-elevation streams accounted for 55% of the total abundance, but accounted for 74% of the losses of brook trout; and streams in the 34° N class accounted for 22% of the total abundances, but incurred 33% of the losses (results not shown). However, these patterns were not absolutely clear in all cases, nor were the patterns always consistent across species.

The regional scale of our study prevented the incorporation of site-specific aspects of streams into the analysis, limiting our interpretations of trout responses to climate change. We assumed that the same width-to-depth relationship, pool and riffle lengths, and invertebrate drift densities applied to all streams in the region, but, in actuality, these vary with stream order and other factors. In lieu of detailed information on

which streams were sympatric and which were allopatric, we assumed that all were potentially sympatric. We attempted to check the robustness of this assumption by comparing predicted changes between the extremes of all streams being sympatric and all streams being allopatric. However, streams in the southern Appalachians contain both sympatric and allopatric populations of brook and rainbow trout (Flebbe 1994), and allopatry can arise for a variety of reasons, some of which could be affected by climate change. Furthermore, model simulations under baseline and climate change generally produced either sympatry or neither species persisting; rarely were streams predicted to be allopatric. Thus, the model is not a good predictor of species composition changes. Meisner (1990) suggested that global climate changes would exacerbate rainbow trout encroachment and increase their dominance in the southern Appalachians. Model simulations show a 61% decrease in abundance (and 90% loss of habitat) of brook trout in headwater streams, which are critical refuges for native brook trout populations (Kelly et al. 1980, Larson and Moore 1985, Larson et al. 1995). Unlike a traditional metapopulation model, our simulations did not include exchanges between populations inhabiting different streams. Movement of individuals between nearby streams appears to be quite variable across the southern Appalachians, and may be one reason that a mix of allopatric and sympatric populations are observed (Larson et al. 1995). While the role of interstream exchange of individuals is unknown, most evidence for the southern Appalachians has shown trout movement to be very limited (Whitworth 1980, Whitworth and Strange 1983, Larson et al. 1995). Hence, while our assumption of no mixing between streams is reasonable, our analyses may underestimate some factors relating to rainbow trout encroachment.

We assumed that all brook trout and all rainbow trout were phenotypically identical across the region. Empirical information on any reproductive, behavioral, or bioenergetics differences in either species across the region was lacking. Differences in early life stage survival and fecundity have been used to explain the increasing dominance of brook trout at northern latitudes (Lennon 1967, Clark and Rose 1997a). McCracken et al. (1993) found significant genetic differentiation between northern strains and southern strains of trout in the Appalachians, although how these differences relate to differences in biology is unknown.

The technology is now available for performing biologically realistic predictions of regional-scale responses to climate change and to other disturbances. We have shown that linking a detailed, realistic biological model with a geographic information system (GIS) database offers a promising tool for performing regional assessments. Individual-based modeling offers an approach for realistically simulating population and community dynamics on a system-specific basis (DeAngelis et al. 1994). The effects of many distur-

bances are often reported as individual-level responses, which can be directly imposed in an individual-based model. The growing use of GIS, and geo-referencing of data, enables estimation of the environmental and other variables needed to apply the individual-based model to the many systems in the region of interest.

Performing regional-scale analyses with detailed biological models also has its disadvantages. Greater complexity in models does not necessarily result in more accurate and precise predictions, and highly detailed models can lead to a false confidence in model forecasts. Application of individual-based models to many sites will likely involve some loss of site specificity. Individual-based models are parameter intensive and may require rarely available information on the biology of the species (e.g., genetics) and how the biology varies across the region. Furthermore, computation costs can be constraining when large databases and complex spatial environments are simulated. Whether to use a detailed individual-based model, or more simple static measures of habitat change, depends on the available data and the goals of the assessment. Our results demonstrate that trout populations in the southern Appalachians may respond to potential global climate changes far differently than predictions based on single variable-temperature models, because interactions among individuals and space involved complex relationships with temperature and flow. As GIS databases become widespread and computing power continues to increase, analyses like those performed here offer a promising tool for regional assessments that involve complex biological and environmental interactions.

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