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[Article]

Survival and Dispersal of Hatchery-Raised Rainbow Trout in a River Basin Undergoing Urbanization

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Abstract.—We evaluated the effect of urbanization on water temperature and the survival of rainbow trout *Oncorhynchus mykiss* that support a popular coldwater fishery in the Chattahoochee River near Atlanta, Georgia. Using multistratum tag recovery models, we estimated the monthly survival, dispersal, and angler harvest reporting rates of stocked trout in two study reaches from March to October 2006. The best-approximating models indicated that the monthly survival of stocked trout was negatively related to angler effort and the amount of time that water temperature exceeded 20°C. We found that trout survival was more sensitive to high water temperature than to angler effort. Dispersal rates from a warmer downstream to a cooler upstream reach were 6–7 times those from upstream to downstream. Empirical temperature–discharge models indicated that water temperatures in the river downstream of Morgan Falls Dam have increased from 1976 to 2006, urbanization being a likely contributing factor. We estimate that on average 60 m^3/s of additional discharge in summer are needed under current (2006) conditions to maintain water temperatures similar to those prior to urbanization (1976). Increased water use from the river accounted for less than one-fourth of the 60 m^3/s, suggesting that other factors, such as a higher percentage of impervious surfaces, were primarily responsible for the higher temperatures. Using these models, we estimate that on average 20% of the stocked trout were lost during the summer months owing to angling and other sources (e.g., high temperature) under preurbanized conditions, whereas 70% of the fish are lost under current conditions. Our models suggest that increasing the hypolimnetic releases from an upstream dam could mitigate the effects of urbanization on water temperature during the summer.

The increase in urban and suburban development is a global problem for aquatic resource managers. During the past decade, urban growth has increased dramatically in the southeastern United States (U.S. Census Bureau 2004), potentially threatening the unique aquatic fauna in the region, as well as managed sport fish populations. The resulting land use conversion and associated increases in water use can alter the dynamics of fish populations and communities, particularly in sensitive coldwater fisheries.

Metropolitan Atlanta, Georgia, and the area surrounding it is a useful example of how changing land use can alter the dynamics of coldwater fisheries. In the last 30 years, urban development has increased by more than 300% (NARSAL 2006) in the counties surrounding the Chattahoochee River National Recreation Area (CRNRA), which contains one of the southernmost trout fisheries in North America. Suitable water temperatures for the fishery are generally maintained year-round owing to hypolimnetic releases from Buford Dam, a large hydroelectric facility at the upstream end of CRNRA (Figure 1). However, with the increasing amount of impervious surface area (e.g., pavement and rooftops) that accompanies urban development, the ability of hypolimnetic water releases to mitigate summer warming trends may diminish. As more urban development occurs, surface water inputs from precipitation during the summer become increasingly warmer (Ferguson and Suckling 1990) because runoff is warmed by remaining on the surface and is discharged into the river faster than would have occurred historically (Paul and Meyer 2001). Instead, impervious surfaces inhibit the ability of storm water to reach cool subterranean strata and recharge groundwater; thus, sources of cool groundwater input can be lost (Ferguson and Suckling 1990; Finkenbine et al. 2000; Wang et al. 2003; Krause et al. 2004). The resulting change in the temperature regimes could affect coldwater fisheries by decreasing fish survival and altering large-scale fish dispersal patterns.

Our goal was to gain an understanding of the manner in which urbanization and water temperature affected

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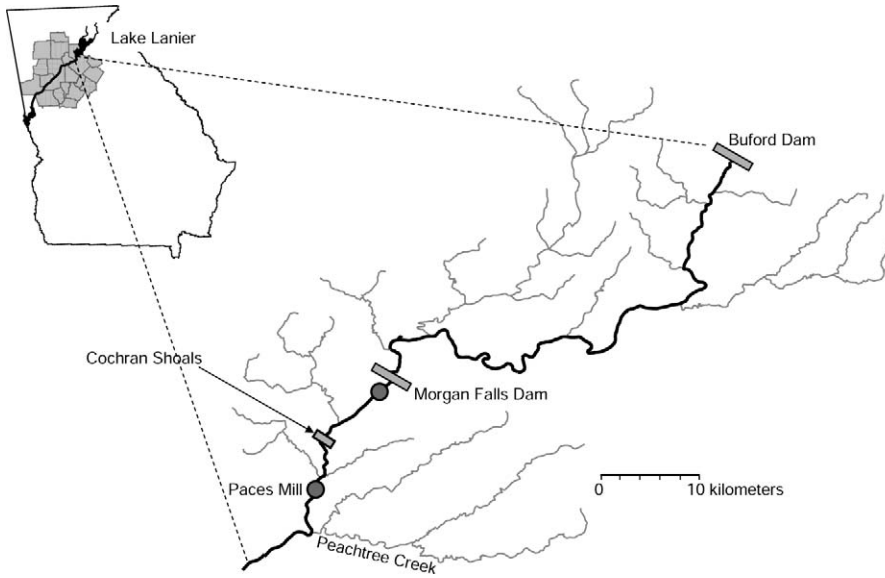

FIGURE 1.—Locations of the Chattahoochee River, Lake Lanier, the upstream and downstream study reaches, and Buford and Morgan Falls dams. The counties comprising metropolitan Atlanta are shaded. The boundaries between the upstream and downstream study sites are Cochran Shoals and Peachtree Creek, respectively; trout stocking locations are indicated by circles.

trout survival in a coldwater fishery and to suggest potential remedial actions. To do so, we examined the effect of summer water temperatures on survival and dispersal of hatchery-raised rainbow trout *Oncorhynchus mykiss* in two adjacent reaches of the Chattahoochee River: an upstream reach with moderate runoff from urbanized areas and a downstream reach with greater amounts of urban runoff. We hypothesized that several factors affect fish survival. First, we proposed that angling pressure decreases fish survival in both reaches. Second, we expected that increases in summer water temperature has a negative effect on trout survival. In terms of large-scale (between-reach) dispersal, we hypothesized several patterns related to water temperature, discharge, and location (i.e., study reach). First, we hypothesized that dispersal is both active and passive (i.e., during times of high temperature in the summer, fish in the downstream reach disperse actively to the cooler upstream reach, but when temperatures are low fish in the upstream reach passively disperse downstream). Second, we hypothesized that dispersal is a one-way active process in which fish sought the cooler upstream regions regardless of water temperature in downstream reach. Finally, we hypothesized that dispersal is passive when fish are continually pushed into the downstream reach and that the dispersal rate increases during times of high discharge.

We combined the rainbow trout survival and dispersal model with empirical stream temperature models under historical (1976) and current (2002–2006) land use conditions. By estimating the loss of stocked trout under the two land use scenarios, we were able to estimate the effect of urbanization on the trout fishery.

Methods

Study site.—Our study took place on the Chattahoochee River between Atlanta, Georgia, and Morgan Falls Dam (river kilometer 487–502, measuring from the mouth of the river) within the CRNRA. We divided the site into two adjacent reaches, Cochran Shoals (33°15′36″N, 84°26′16″W) marking the boundary between the reaches (Figure 1). The upstream reach was 8.1 km long, drained 3,548 km^2, and had an average annual discharge of 59.3 m^3/s; the downstream reach was 6.4 km long, drained 3,755 km^2, and had an average annual discharge of 70.8 m^3/s. The upstream reach consisted primarily of pool-and-run habitats and smaller amounts of shoal habitats, whereas the downstream reaches contained greater amounts of shoal habitats and fewer pool-and-run habitats. Four municipal water supply intakes are located on the river, two above Morgan Falls Dam, and the other two are located on the upper and lower study reaches.

Water temperatures in this section of the Chattahoochee River are influenced by releases from both Morgan Falls Dam (0 km upstream from the upper end

of the study site) and Buford Dam (58 km upstream; Figure 1), as well as by surface water inputs from precipitation events from several tributaries located downstream of Buford Dam (Georgia Power 2006). Buford Dam impounds Lake Lanier (153.8 km^2) and releases cold hypolimnetic water from a depth of 48.8 m that exerts the greatest influence on the water temperature downstream of the dam (Georgia Power 2006). In contrast, Morgan Falls Dam impounds a much smaller (2.69 km^2) and shallower (maximum depth, 4.1 m) lake and currently is operated as a run of the river dam. Thus, this dam does not provide hypolimnetic inputs to the system.

Mark–recapture sampling design.—Marked and unmarked hatchery-raised rainbow trout were released at a single location in each study reach (Figure 1) approximately monthly from March to September 2006 and at a rate of 300–410 fish/month. The trout (catchable size, averaging 228 mm total length) were marked with uniquely numbered Floy tags, colored elastomer injections (unique to stocking date and location), or both types approximately 1 month before stocking. After being marked, fish were held at the hatchery to estimate tag retention rates and survival. The Floy tags included contact information so anglers could report a tagged fish. Anglers were asked the tag number, date of catch, location of catch, and whether the fish was released (with the tag still inserted or with the tag removed) or harvested.

Fish were sampled for the three consecutive days after the release of the hatchery fish. Within each study reach, we established nine fish sampling sites that were uniformly distributed along the reach. During each sampling day, we sampled each site for 10 min using a boat-mounted, dual-electrode Wisconsin ring electrofisher (Reynolds 1996) operating at approximately 3 A of pulsed direct current for a total 1.5 h of pedal time (current on) per reach; however, on a few occasions, we were only able to complete 1 h per reach. We adjusted for this unequal sampling effort by modeling electrofishing capture probabilities as a function of effort (hours of pedal time per sampling period). Captured fish were identified, checked for a tag or elastomer mark, and released. The elastomer marks (unique for study reach and date) allowed us to differentiate individuals that had been never been recaptured from those that had been.

To estimate angler effort, we conducted a concurrent bus stop access creel survey (Robson and Jones 1989; Jones et al. 1990) for completed trip information. The river was divided into three areas with three to five access points in each area. The creel started April 1, 2005, and was completed September 30, 2006. The day was divided into morning and afternoon periods. We used 14-d intervals within which 10 d were sampled, including all weekend days. The creel clerk informed anglers of the tagging study and encouraged them to report tagged trout. He also provided stamped, self-addressed envelopes to encourage reporting. Pertinent data recorded included the hours fished, fishing method (bank, boat, or wading), target species, species caught, and number of fish caught. We then used these data to estimate the total number of angler-hours at each study reach for the period between sampling occasions. Because the creel ended in September, we fit a linear regression model between angler-hours and reported number of fish caught from March to September and then used the reported number of fish caught in October to predict angler-hours in October. This predicted value was used in the survival estimation modeling detailed below.

To evaluate the influence of river discharge and water temperature on the survival and dispersal of rainbow trout, we obtained data recorded at 15-min intervals from two U.S. Geological Survey (USGS) water quality monitoring stations located at the upstream reach (station 02335810) and the downstream reach (02336000). Using these data, we estimated average and maximum temperature and discharge for the period between monthly fish sampling. We were primarily interested in estimating the effect of chronic (long term) temperatures on trout survival rather than acute lethal temperatures. Water temperature influences long-term fish survival by altering their vulnerability to predation (Coutant 1973) and pathogens (Hbtrick et al. 1979) and through interspecific interactions such as competition (Cunjak and Green 1986; Reese and Harvey 2002). The effect of these interactions is probably minimized when temperatures are within the optimal or preferred temperature (Reese and Harvey 2002). Thus, we estimated the total number of 15-min intervals that temperatures exceeded 20°C (hereafter termed "exceedance") for the periods between monthly fish sampling trips; we selected 20°C based on the reported upper limits of rainbow trout preferred and optimal temperatures (Coutant 1977; Hokanson et al. 1977).

Statistical analysis of mark–recapture.—We used a multistratum, tag recovery model (Barker and White 2001) implemented in program MARK (White and Burnham 1999) to estimate rainbow trout survival and dispersal in response to temperature and flow patterns. Here, the strata are the two study reaches. These models produce four types of probability-based estimates: survival, movement, recapture, and reporting. Survival (S) is defined as the probability of an individual's surviving between sample periods (defined as 1-month intervals for this study). Movement (ψ) is

the monthly probability that an individual will move from one reach to another, given that it survived. Recapture (p) is the probability that an individual will be recaptured by biologists or caught and released by anglers, and reporting (r) is the probability that a tag will be reported by anglers given that a fish was harvested.

From water quality monitoring stations, we obtained data on maximum discharge and water temperature, average discharge and water temperature for a given month, and the total number of exceedances. We used the number of exceedances as an index to water temperature because exceedance measures are currently used by local management agencies to make management decisions regarding rainbow trout. We used average discharge per month because we believed this would better correspond to both survival and dispersal rate parameters rather than the extremes represented by maximum discharge.

For the model selection process, we formulated a set of a priori models that specified the variables potentially affecting model parameters. We then fit every model in the resulting model set. To investigate the factors influencing monthly trout survival, we fit models with the following predictor variables: reach, angler effort, temperature exceedance, and average discharge for the month before fish sampling. The global (most highly parameterized) model for survival was (reach $\times$ exceedance) $+$ angler effort $+$ average discharge. We evaluated factors influencing large-scale (between-reach) fish movement by considering direction of movement, temperature exceedance, and average discharge for each month. We note that the system was essentially closed; that is, Morgan Falls Dam prevented dispersal upstream from the study system, and summer water temperatures resulted in mortality of any downstream dispersers. Thus, we estimated two parameters for directional dispersal: movement from upstream to downstream strata and vice versa. The most saturated models (most predictors) for ψ were direction $\times$ exceedance and direction $\times$ average discharge. We lacked the data to fit a global model with both terms. The direction $\times$ exceedance model represents the hypothesis that trout move from the downstream to the upstream (cooler) reach in response to temperature much more readily than they would move from the upstream to the downstream reach. The direction $\times$ average discharge model represents the hypothesis that dispersal was related to discharge. The capture probability was modeled as a constant or as a function of the number of hours of pedal time per month that biologists sampled. Catch and release angling could also affect the estimate of capture probability because fish that were caught and released were included as recaptures in the input data. However, 85% of recaptures were by biologists; thus, we believe biologist effort would capture most of the temporal variation in this estimate. Finally, the reporting parameter was modeled as constant across time and reaches because we could conceive no reason why anglers would change their reporting rate across the length of the study or across the locations of catch.

We evaluated the relative fit of candidate models of trout survival and movement by calculating Akaike's information criterion (AIC; Akaike 1973), ΔAIC, and Akaike weights (Burnham and Anderson 2002) that range from 0 to 1, the larger values indicating better-fitting models. We summed Akaike weights to compare the weight of evidence regarding two hypotheses: whether temperature (exceedance) affected dispersal and whether electrofishing effort affected the probability of recapture. For these comparisons, we summed equal numbers of models for each hypothesis.

To incorporate model selection uncertainty for the tag recovery models, we used Akaike weights to calculate model-averaged parameter estimates and unconditional standard errors (following Burnham and Anderson 2002). We based all inferences and predictions on model-averaged parameter estimates and assessed the precision of model-averaged parameter estimates by calculating 95% confidence intervals (CIs).

Estimating the effect of urbanization.—Estimating the effect of urbanization on the trout fishery in the Chattahoochee River required estimates of the change in the yearly number of exceedances that occurred during the summer months, after accounting for the effects of discharge and climate (i.e., temperature and precipitation). Thus, we fit models relating discharge, air temperature, and precipitation to the number of exceedances occurring in a 24-h period using historical and current daily data. We obtained water temperature data from the USGS water quality station (02336000) located at the downstream study reach for the years 1976, 2002, and 2004–2006 and supplemented these with our own measurements collected at the same location from 1991 to 1993, 1999, and 2003. To examine the relationship between Buford Dam discharge and water temperature at the downstream study reach, we constrained our analysis to the months June–August, when we expected exceedances to occur. For 2002 and 2004–2006, the data were collected in 15-min intervals. From 1991 to 1993, the data were collected in 30-min intervals. For 1999 and 2003 the data were collected in hourly intervals. To transform these hourly and 30-min data, we summed the number of exceedances per day and multiplied this sum by four (hourly data) or two (30-min data) to obtain an estimate

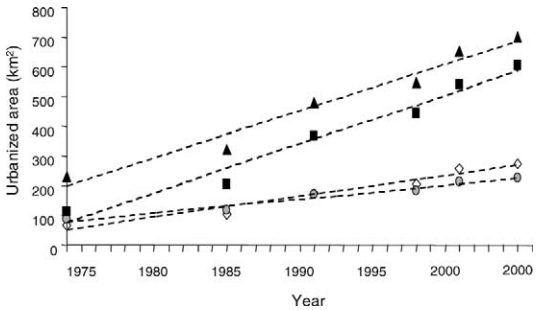

FIGURE 2.—Changes in urban land use for the four counties adjacent to the study area from 1974 to 1905. The lines represent least-squares fits for urban land use in Cobb (diamonds), DeKalb (circles), Fulton (triangles), and Gwinnett (squares) counties (data from NARSAL 2006).

of the daily number exceedances if measured at 15-min intervals. For 1976, the only data available for water temperature were daily values, such as maximum, mean, and minimum. To transform the 1976 data from maximum daily temperature to the number of 15-min exceedance intervals per day, we performed a linear regression (Neter et al. 1990) on the 2004–2006 data for which both exceedance and maximum daily water temperature were known.

To investigate the effect of Buford Dam releases and urbanization on water temperature in the downstream study reach, we fit candidate linear regression models relating discharge at Buford Dam, daily precipitation, and maximum air temperature to daily exceedances at the downstream study reach. As with the mark–recapture process, all models were formulated a priori and then fit. Candidate models included 1-d and 2-d lags between the discharge at Buford Dam and daily exceedances, based on information from Georgia Power (2006) that water temperatures below Buford Dam are strongly related to water temperatures above Morgan Falls Dam 12 h later. We included the daily maximum air temperature at Hartsfield–Jackson Atlanta International Airport (24 km from the study site) and the daily precipitation at the National Oceanic and Atmospheric Administration Atlanta–Bolton weather station (4.3 km from the study site) as covariates in every model. Candidate models also included year as a predictor variable and year–discharge, year–precipitation, and year–temperature interactions to examine whether the relationships have changed with urbanization in the region from 1976 to 2006. This required the assumption that urbanization increased linearly during this period, which was supported by plots of urban land use change for the four counties that were adjacent to the study area (Figure 2). We coded 1976 as the intercept (baseline) for the year term and compared relative fit of the candidate models by calculating the AIC, ΔAIC, and AIC weights. Goodness of fit was assessed for the best-approximating models by examining residual and normal probability plots.

To predict the effects of urbanization on trout loss, we used the best-approximating models from both the discharge–exceedance and survival analyses. For the discharge–exceedance model, we estimated total monthly exceedance using average daily values for maximum air temperature, precipitation, and discharge from Buford Dam observed from 1991 to 2006. For the preurbanization scenario, we estimated expected exceedances based on a year term = 1976 and for the urbanization scenario with the year = 2007. This resulted in two sets of predicted daily exceedances. We summed these predicted daily exceedances over each month and used these values along with the estimated relationship between survival and exceedances obtained from the mark–recapture model to estimate monthly trout mortality. We assumed that mortality equaled 1 minus survival for summer months because trout in this system could not emigrate successfully (i.e., emigration upstream was blocked by Morgan Falls Dam and emigration downstream would be lethal owing to water temperatures >25°C). We then used the mortality estimates and Georgia Department of Natural Resources stocking records from 1991 to 2006 to predict the number of trout lost to urbanization. Finally, we predicted trout mortality under a range of discharges from Buford Dam for preurbanization (1976) versus current conditions (2006; based on air temperature and precipitation data for 2006). The estimates were for discharges at Buford Dam that ranged from 12 to 237 m^3/s, the minimum and maximum discharges observed during summer months.

We evaluated the effect of increased water use on the discharge at the downstream study reach by fitting candidate linear regression models relating daily discharge at Buford Dam to daily discharge at the downstream study reach for the preurbanization (1976–1980) and current (2002–2006) periods. Similar to the exceedance models, candidate models included 1-d and 2-d lags between the discharge at Buford Dam and discharge at the downstream reach. Candidate models also included a binary indicator for the current versus the preurbanization period and a period–discharge interaction to examine whether the relationships have changed with urbanization. We compared relative fit of the candidate models by calculating AIC and ΔAIC. Goodness of fit was assessed for the best-approximating model by examining residual and normal probability plots.

TABLE 1.—Rainbow trout angling pressure, discharge, and stream temperature in the Chattahoochee River, Georgia, by study reach and month.

	Upstream reach		Downstream reach	
Period	Mean (SD)	Range	Mean (SD)	Range
		Angler effort (number/d)		
Mar	11.09 (22.18)	0–44.4	54.21 (79.49)	0–274.7
Apr	58.06 (54.22)	0–112.9	29.91 (29.28)	0–79.7
May	37.57 (37.78)	0–85.4	49.33 (57.90)	0–171.8
Jun	8.06 (16.13)	0–32.3	31.64 (42.74)	0–153.1
Jul	39.73 (40.18)	0–91.5	21.24 (32.79)	0–119.0
Aug	36.59 (51.74)	0–73.2	24.53 (33.67)	0–115.6
Sep	16.13 (36.07)	0–80.6	20.24 (35.45)	0–131.0
		Discharge (m^3/s)		
Mar	52.90 (25.13)	28.7–176.9	66.00 (34.65)	32.5–233.5
Apr	55.49 (24.97)	28.2–167.7	67.27 (29.13)	32.8–167.9
May	60.40 (29.48)	29.3–196.6	69.56 (33.79)	30.5–206.2
Jun	44.52 (21.31)	27.4–195.7	50.32 (25.44)	27.1–186.6
Jul	32.46 (7.70)	24.8–80.1	33.09 (8.57)	22.8–99.6
Aug	38.65 (12.23)	26.7–107.2	40.51 (13.36)	28.0–103.3
Sep	38.29 (14.08)	28.2–116.1	39.36 (14.69)	27.3–120.3
Oct	38.73 (19.99)	27.5–196.2	40.37 (21.86)	27.1–194.1
		Temperature (°C)		
Mar	11.59 (1.61)	9.0–16.2	11.95 (1.78)	8.5–17.1
Apr	14.91 (1.90)	11.4–19.9	15.67 (1.97)	12.4–21.6
May	15.27 (2.28)	10.9–21.6	16.29 (2.57)	12.2–23.2
Jun	18.20 (2.02)	12.0–22.2	19.64 (2.11)	14.4–24.4
Jul	20.12 (1.39)	16.9–24.9	22.04 (1.61)	18.5–27.7
Aug	19.88 (1.19)	16.5–23.5	21.77 (1.50)	17.5–25.6
Sep	17.85 (1.24)	14.9–21.5	19.10 (1.50)	14.9–23.3
Oct	15.00 (1.86)	10.8–18.2	15.62 (2.22)	10.8–20.4

Results

We released 14,400 rainbow trout, 5,819 of which were marked. Of these, 3,988 were marked with Floy (FD-68B) tags, 2,080 were marked with elastomer only, and 357 were marked with both. Biologists recaptured 113 of the marked trout at least once; anglers reported catching and releasing 29 marked fish and harvesting (retaining) 35 marked fish. Tag retention rates 1 month after tagging averaged 97.8% and were lower for the elastomer (89.8%) than the Floy tags (99.5%). One-month survival for tagged fish before stocking averaged 89.9%.

Angler effort during the study was, on average, greatest during the spring and lowest during the summer (Table 1). However, there was considerable overlap between the amounts of angling pressure at each study reach. Discharge at Buford Dam and river water temperature were inversely related, discharge being highest and temperature lowest during the spring. Discharge and temperature also were, on average, greater at the downstream reach, where maximum temperatures during July and August reached reported lethal temperatures (25°C; Cherry et al. 1977) for rainbow trout.

Mark–Recapture

The best-approximating multistratum, tag recovery model (Table 2) contained the variables S(exceedance + angler effort), p(effort), ψ(directional), and a constant reporting rate probability, r(.). This model was 2.0 times as likely to be the best-approximating model as the next-best model, which differed only by omitting the effort term from the electrofishing recapture probability. Evidence ratios based upon Akaike importance weights suggested that models without the effect of temperature on dispersal were 1.8 times more likely to explain the data than models with the temperature effect (Table 3). Of the dispersal models with no temperature effect, the direction-specific models were 4.1 times more likely to explain the data than models with dispersal randomly occurring between upstream and downstream sites. Evidence ratios also suggested that capture probability models with electrofishing effort were 2.1 times more likely to explain the data than models in which capture probability was assumed constant (Table 3). Five of the six best-approximating models had survival varying with exceedance and angling pressure only (Table 2).

The estimated rates of survival decreased during summer (Figure 3), especially in the downstream reach,

TABLE 2.—Number of parameters (K), relative Akaike information criterion values (ΔAIC), and Akaike weights (w) for the candidate multistratum models for estimating the probabilities of rainbow trout survival (S), dispersion (ψ), and recapture (p) in two study reaches on the Chattahoochee River, Georgia. The models included here had an Akaike weight of at least 0.01. All models included a term for probability of being reported that is not shown. See text for more on model variables.

Model[a]	K	ΔAIC	w
S(exceedance + angler effort), p(effort), ψ(directional)	8	0.000	0.178
S(exceedance + angler effort), p(.), ψ(directional)	7	1.445	0.087
S(reach + exceedance + angler effort), p(effort), ψ(directional)	9	1.493	0.085
S(exceedance + angler effort), p(effort), ψ(directional + exceedance)	9	1.999	0.066
S(exceedance + angler effort), p(effort), ψ(directional × exceedance)	10	2.466	0.052
S(exceedance + angler effort), p(effort), ψ(.)	7	2.502	0.051
S(reach + exceedance + angler effort), p(.), ψ(directional)	8	3.084	0.038
S(reach × exceedance + angler effort), p(effort), ψ(directional)	10	3.216	0.036
S(exceedance + angler effort), p(effort), ψ(directional × average discharge)	10	3.387	0.033
S(exceedance + angler effort), p(.), ψ(directional + exceedance)	8	3.424	0.032
S(reach + exceedance + angler effort), p(effort), ψ(directional + exceedance)	10	3.492	0.031
S(exceedance + angler effort), p(.), ψ(directional × exceedance)	9	3.651	0.029
S(reach + exceedance + angler effort), p(effort), ψ(directional × exceedance)	11	3.839	0.026
S(reach + exceedance + angler effort), p(effort), ψ(.)	8	4.240	0.021
S(reach × exceedance + angler effort), p(.), ψ(directional)	9	4.440	0.019
S(exceedance), p(effort), ψ(directional)	7	4.670	0.017
S(exceedance + angler effort), p(.), ψ(.)	6	4.783	0.016
S(reach + exceedance + angler effort), p(effort), ψ(directional × average discharge)	11	4.853	0.016
S(exceedance + angler effort), p(.), ψ(directional × average discharge)	9	4.974	0.015
S(reach + exceedance + angler effort), p(.), ψ(directional + exceedance)	9	5.057	0.014
S(reach × exceedance + angler effort), p(effort), ψ(directional + exceedance)	11	5.214	0.013
S(reach + exceedance + angler effort), p(.), ψ(directional × exceedance)	10	5.229	0.013
S(exceedance), p(.), ψ(directional)	6	5.448	0.012
S(reach × exceedance + angler effort), p(effort), ψ(directional × exceedance)	12	5.636	0.011

[a] (.) indicates that the parameter was modeled as a constant.

where water levels were low and temperatures were high during summer 2006. The decrease in survival was primarily due to the influence of increased number of exceedances during summer months (Figure 4) because angler effort decreased in the downstream reach in summer (Table 1), which we would expect to increase survival. Model-averaged estimates indicated that both angler effort and exceedance intervals influenced rates of survival (Table 4). We estimate that survival was, on average, 1.03 times lower for each 1 h increase in angler effort, whereas survival was 1.1 times lower with each single unit increase in exceedance. Thus, the effect of exceedance on survival was greater than the effect of angler effort (Figure 4). There also was some evidence that survival differed among study reaches. The parameter estimates for reach differences, however, were relatively imprecise, and the confidence intervals for all reach effects contained zero (no effect).

TABLE 3.—Akaike importance weights for hypotheses regarding rainbow trout dispersal and recapture probabilities in the Chattahoochee River.

Hypothesis	Akaike weight	Number of models	Evidence ratio
Dispersal (ψ)			
Temperature effect			
None	0.590	16	1.8
Effect realized	0.324	16	
Directional effect			
None	0.116	8	
Direction-specific	0.474	8	4.1
Recapture (p)			
Electrofishing effect			
None	0.325	20	
Effect realized	0.675	20	2.1

Dispersal between study reaches tended to occur more from downstream to upstream areas than vice versa (Figure 3b). Model-averaged estimates indicated that upstream dispersal averaged just above 0.06 for the study period, whereas downstream dispersal averaged just under 0.02. Although 95% CIs on direction-specific dispersal were large and overlapped (Table 4; Figure 3b), Akaike importance weights indicate that models including direction-specific dispersal were better supported by the data, with an evidence ratio of 4.1 (Tables 2, 3).

Effects of Urbanization

The best-approximating model for estimating exceedance at the downstream reach from 1976 to 2006 included terms for discharge at Buford Dam with a 1-d lag (hereafter "discharge"), year, daily precipitation, maximum daily air temperature, a discharge quadratic term, and a discharge–year interaction (Table 5). The model was 1.31 times more likely than the next-best

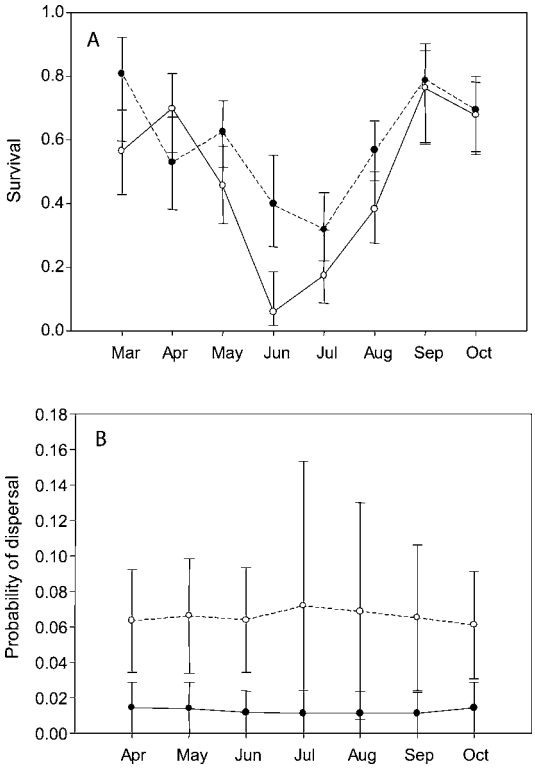

FIGURE 3.—Model-averaged estimates and 95% confidence intervals for **(a)** hatchery-raised rainbow trout monthly survival in the upstream (filled circles) and downstream (open circles) study reaches and **(b)** upstream (open circles) and downstream (filled circles) dispersal rates in the Chattahoochee River from March to October 2006.

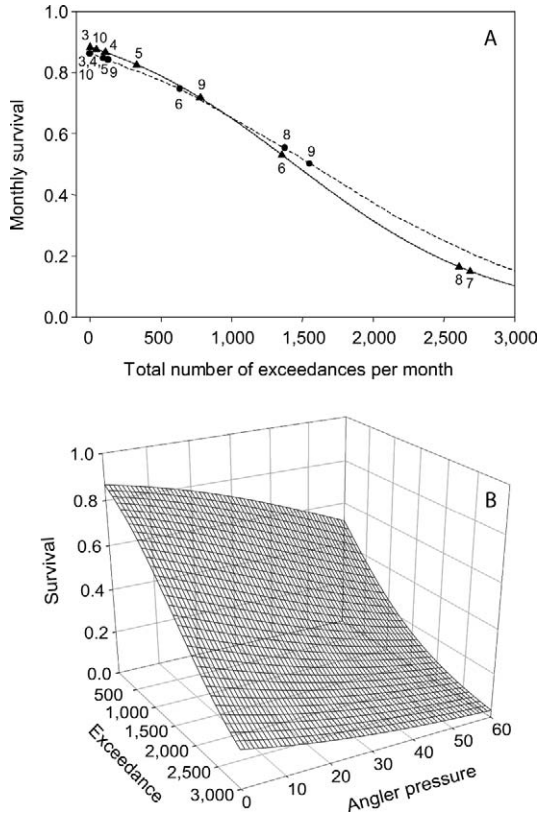

FIGURE 4.—Model-averaged estimates of **(a)** monthly rainbow trout survival versus the number of exceedances at the upstream (circles, broken line) and downstream (triangles, solid line) study reaches and **(b)** the effect of exceedances and angler effort on rainbow trout survival in the Chattahoochee River. The numbers in panel (a) represent the months in which exceedance measures were recorded at each reach (e.g., 6 = June).

model, which was similar but contained a daily precipitation–year interaction. Parameter estimates from the best-approximating model indicate that for every cubic meter of water released at Buford Dam in 1976, an estimated 1.16 fewer exceedance intervals occurred per day in the downstream reach. By comparison, the discharge–year interaction indicated that for every year after 1976, a greater volume of water was required to maintain preurbanization water temperatures (Table 6). Similarly, the precipitation–year interaction in the second-best model suggested that for every progressive year since 1976, 1 cm of rain caused, on average, 0.12 more exceedance intervals per day, though the 95% CIs were relatively large and contained 0 (Table 6).

Assuming average daily values from 1991 to 2006 for precipitation, maximum air temperature, and discharge, we estimate that 40 more water temperature exceedances occur per day under current conditions than under preurbanization conditions. The greater number of exceedances also had a substantial influence on the trout fishery at the downstream reach. We estimate that given average daily values from 1991 to 2006 for precipitation, maximum air temperature, and discharge, 20% of stocked trout were lost during the summer months from angling or other sources (e.g., high temperature) under preurbanized conditions, whereas 70% of fish would be lost under current conditions (Figure 5a). These values equate to a loss of 6,643 stocked fish under preurbanization conditions and 22,762 under current conditions, assuming the average stocking levels from 1991 to 2006. We also estimate that greater discharges are needed at Buford Dam to maintain equivalent trout mortality rates under current conditions compared with preurbanization conditions (Figure 5b).

TABLE 4.—Model-averaged parameter estimates, standard errors, and 95% confidence intervals (CIs) of rainbow trout survival, recapture, dispersal, and recovery probabilities. The models used to calculate these estimates are in Table 2.

Parameter	Estimate[a]	SE	95% CI
Survival			
Intercept	1.81	0.66	(0.51, 3.11)
Reach	0.20	0.28	(−0.35, 0.75)
Angler effort (h/d)	−0.03	0.01	(−0.06, 0.00)
Exceedance (number/month)	−0.12	0.03	(−0.17, −0.06)
Reach × exceedance	−0.02	0.04	(−0.10, 0.05)
Recapture			
Intercept	−4.27	0.90	(−6.03, −2.51)
Effort	0.05	0.03	(−0.00, 0.11)
Dispersal			
Intercept	−4.47	1.72	(−7.84, −1.11)
Direction	1.86	1.87	(−1.81, 5.52)
Exceedance	−0.49	1.36	(−3.17, 2.18)
Direction × exceedance	1.11	1.86	(−2.53, 4.75)
Average discharge (m^3/s)	0.03	0.10	(−0.17, 0.22)
Direction × average discharge	0.01	0.10	(−0.21, 0.20)
Reporting			
Intercept	−4.87	0.17	(−5.21, −4.53)

[a] Parameter estimates are on a logit scale.

TABLE 6.—Parameter estimates, standard errors, and 95% confidence intervals (CIs) for the two best models for estimating the number of 15-min intervals per day with temperatures greater that 20°C at the downstream study reach on the Chattahoochee River.

Parameter[a]	Estimate	SE	95% CI
Best model			
Intercept	−30.76	9.69	(−49.75, −11.76)
Q-lag1	−1.16	0.08	(−1.32, −1.00)
Maximum daily air temperature (°C)	2.57	0.29	(2.00, 3.14)
Daily precipitation (cm)	0.99	0.80	(−0.58, 2.57)
Year	2.50	0.17	(2.18, 2.83)
Q-lag1^2	0.01	0.01	(0.00, 0.01)
Q-lag1 × year	−0.02	0.00	(−0.02, −0.02)
Second-best model			
Intercept	−29.10	9.78	(−48.27, −9.93)
Q-lag1	−1.15	0.08	(−1.31, −0.99)
Maximum daily air temperature (°C)	2.54	0.29	(1.97, 3.11)
Daily precipitation (cm)	−1.97	2.59	(−7.05, 3.11)
Year	2.46	0.17	(2.13, 2.79)
Daily precipitation × year	0.12	0.10	(−0.08, 0.33)
Q-lag1^2	0.01	0.01	(0.00, 0.01)
Q-lag1 × year	−0.02	0.01	(−0.02, −0.02)

[a] Q-lag1 = discharge (m^3/s) at Buford Dam 1 d before water temperature reading.

The best-approximating model for estimating stream discharge at the downstream reach during the preurbanization and current periods included discharge at Buford Dam with a 1-d lag and a current period indicator variable × discharge interaction. The parameter estimates indicate that discharges at the downstream reach in June–August under current conditions do not differ from those under preurbanization conditions during low flows but are greater during high flows (Table 7).

Discussion

Water temperatures during the summer strongly affected the survival of stocked rainbow trout in the Chattahoochee River. The negative effect of warm

TABLE 5.—Number of parameters (K), relative Akaike information criterion values (ΔAIC), and AIC weights (w) for the set of models for estimating the number of 15-min intervals with temperatures greater that 20°C at the downstream study reach on the Chattahoochee River.

Model[a]	K	ΔAIC	w
Maximum daily air temperature, daily precipitation, Q-lag1 × year, Q-lag1^2	8	0.00	0.485
Maximum daily air temperature, Q-lag1 × year, Q-lag1^2, daily precipitation × year	9	0.55	0.369
Q-lag1 × year, Q-lag1^2, daily precipitation × year, maximum daily air temperature × daily precipitation	10	2.40	0.146
Q-lag1, Q-lag1^2, maximum daily air temperature, daily precipitation, year	7	105.16	0
Q-lag1, Q-lag1^2, maximum daily air temperature, daily precipitation × year	8	105.48	0
Maximum daily air temperature, Q-lag1 × year, daily precipitation × year	8	181.97	0
Maximum daily air temperature , Q-lag1 × year	7	183.02	0
Q-lag1, Q-lag1^2, maximum daily air temperature, daily precipitation	6	206.15	0
Maximum daily air temperature, Q-lag2 × year, daily precipitation × year	8	243.61	0
Maximum daily air temperature , Q-lag2 × year	7	250.34	0
Q-lag1, maximum daily air temperature, daily precipitation × year	7	279.09	0
Q-lag1, maximum daily air temperature, daily precipitation, year	6	280.46	0
Q-lag2, maximum daily air temperature, daily precipitation × year	7	317.79	0
Q-lag2, maximum daily air temperature, daily precipitation, year	6	322.37	0
Q-lag1, maximum daily air temperature, daily precipitation	5	374.96	0
Q-lag2, maximum daily air temperature, daily precipitation	5	415.81	0

[a] Q-lag1 = discharge (m^3/s) at Buford Dam 1 d before water temperature reading, and Q-lag2 = discharge at Buford Dam 2 d before.

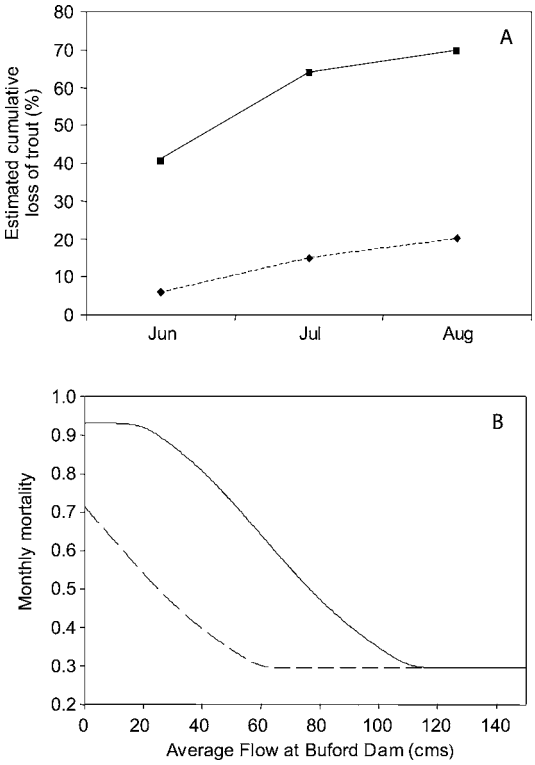

FIGURE 5.—**(a)** The estimated cumulative percentage of rainbow trout in the Chattahoochee River lost per month during summer owing to mortality under preurbanization (1976; broken line) and current (2006; solid line) conditions and **(b)** the monthly mortality of rainbow trout at varying flow rates under preurbanization and current conditions, assuming equivalent air temperature and precipitation (i.e., the average values in summer from 1991 to 2006).

water temperatures on salmonids is certainly not a new finding (e.g., Fry et al. 1946; Hughes and Roberts 1970). However, we also found that water temperatures in the Chattahoochee River downstream of Morgan Falls Dam were increasing yearly, which negatively affected the popular recreational trout fishery. Based on recorded stocking levels, we estimated that 9,400 fewer trout are available, on average, for angling each month under current conditions than under preurbanization conditions, which represents a reduction of about one-third of the stocked trout population. We believe that the increased temperatures were primarily due to urbanization and the concomitant increase in impervious surface, rather than increased water demand. We estimate that, on average, 60 m^3/s of additional discharge is currently needed from Buford Dam to maintain the same level of trout survival at the downstream reach as under preurbanization conditions. The river discharge models also suggest that the

TABLE 7.—Parameter estimates, standard errors, and 95% confidence intervals (CIs) for the two best models for estimating discharge at the downstream study reach during the preurbanization (1976–1980) and current (2002–2006) periods on the Chattahoochee River, Georgia.

Parameter[a]	Estimate	SE	95% CI
	Best model		
Intercept	20.86	3.58	(12.76, 28.97)
Q-lag1	0.80	0.04	(0.72, 0.88)
Q-lag1 × current	0.09	0.06	(−0.03, 0.20)
	Second-best model		
Intercept	20.93	3.81	(12.32, 29.53)
Q-lag1	0.84	0.03	(0.77, 0.90)

[a] Q-lag1 = discharge (m^3/s) at Buford Dam 1 d before.

increased temperatures were not due to increased water use. Impervious surfaces decrease infiltration, which increases surface water runoff directly into the stream, increasing temperatures during warm seasons (Ferguson and Suckling 1990; Wang et al. 2003; Krause et al. 2004). The effect of increased surface runoff is further exacerbated when impervious surfaces, such as roadways and parking lots, are very warm and in turn warm precipitation runoff before it enters the river. This is consistent with the observed precipitation–year interaction in the exceedance–discharge models, which suggests that precipitation under current conditions increases water temperatures more than it did under preurbanization conditions.

Despite the occurrence of lethal water temperatures in the lower study reach, some fish did survive during the warmest months. Physical habitat in this area was of higher quality (i.e., with more riffles, shoals, and deep pools; Nestler et al. 1984), which may have aided fish survival. The more likely mechanism, however, is that this section of the river contains numerous seeps where groundwater enters the river (Couch et al. 1996). The groundwater is cooler (17–19°C) than surface waters during the summer, and hence these areas probably function as thermal refugia (e.g., Kaya et al. 1971). The relative amounts of these thermal refugia are influenced, in part, by infiltration of precipitation into the groundwater (Gordon et al. 1992). Thus, we expect the relative number of refugia to decrease with expanded urbanization, as related to its negative influence on the trout fishery.

In contrast to the temperatures in the lower reach, those in the upper reach did not reach acute lethal levels during the summer. Nonetheless, fish survival was lowest in the upstream reach during summer months and much of this was due to the increased number of exceedances. We believe that this was probably due to chronic effects resulting from frequent but short duration exposure to higher, but sublethal

temperatures. Rainbow trout that are exposed to high but nonlethal temperatures for short durations are more susceptible to predation (Coutant 1973) and pathogens (Hbtrick et al. 1979). Indeed, stocked trout were the most abundant food item in the diet of striped bass *Morone saxatilis* in this section of the Chattahoochee River (Hess and Jennings 2002). Water temperatures also reached 23°C several times during the months of July and August in the upstream reach, sufficient to cause detrimental chronic effects (Bartholow 1991). Our results and those of previous cited studies support the contention that fishery managers should consider the influence of chronic exposure to higher nonlethal temperatures when developing regulations and management strategies.

Increased flows from Buford Dam could mitigate trout loss, but current releases from Buford Dam are insufficient to curtail the effects of increasing impervious surface area. During summers of 2001 to 2006, 19 months (out of a possible 30) experienced average monthly releases less than 20 m^3/s at Buford Dam. Under current urbanization conditions, an average flow of 20 m^3/s will result in less than 10% monthly survival (Figure 5b). Under preurbanization conditions, 20 m^3/s would have resulted in about 45% survival (Figure 5b). Therefore, if current trends in both water release from Buford Dam and increasing impervious surface area in the Chattahoochee River basin continue, we can expect near 0% monthly survival in summer for stocked rainbow trout below Cochran Shoals.

Dispersal

Interestingly, the dispersal patterns of stocked trout suggested that the large-scale (between-reach) movement from the downstream to the upstream reach was 6–7 times that of the downstream movement. This provides evidence against the strategy of passive (downstream) or random dispersal for stocked trout and was surprising, given that trout habitat is better in the downstream reach because of the presence of several large shoal habitats. We also found little evidence that average discharge or exceedance levels influenced trout dispersal. However, given the low number of trout that were recaptured after dispersing, it may have been difficult to estimate the influence of environmental factors, such as temperature and flow, on dispersal with sufficient precision. Salmonids are known to behaviorally thermoregulate (Torgersen et al. 1999; Ebersole et al. 2001; Goniea et al. 2006), which suggests that rainbow trout should seek out areas with the proper temperature. Thus, we hypothesize that decreasing water quality (i.e., increasing temperature) in the downstream reach in summer is primarily responsible for the greater upstream movement.

Past studies have found predominantly downstream movement between reaches for stocked rainbow trout (Cresswell 1981; Helfrich and Kendall 1982; Bettinger and Bettoli 2002), with at least one exception (Hazzard and Shetter 1938). That one study was in the Adirondack Mountains, New York, where dispersal was predominantly upstream one year and downstream the next (Baird et al. 2006). Although no reach-specific temperature differences between years were mentioned in that study, temperature differences certainly could have explained the upstream dispersal we observed. In an Idaho reservoir, downstream dispersal of rainbow trout was related to increased water temperature (Casey 1965). The hypothesis that temperature differences between reaches can reverse the predominant direction of successful dispersal for rainbow trout is intriguing but needs further investigation. Certainly, our analysis supports such a hypothesis, but with only 1 year of data upon which to base this observation, our inferences are limited. This question may be better investigated using a meta-analysis of studies that have measured directional dispersal and temperature differences between reaches.

As discussed earlier, temperatures in the lower reach attained lethal levels during the summer, yet the movement rates from the downstream reach to the cooler upstream reach averaged only 6%. Possibly, the relatively low rates were due to the general inexperience of fish stocked into a new environment. Hatchery trout are naïve and their general tendency is to disperse downstream (Cresswell 1981; Helfrich and Kendall 1982), especially when discharge is high (Bettinger and Bettoli 2002). Thus, two competing forces may exist, the desire to behaviorally thermoregulate (move upstream) and the general inexperience of the fish. Perhaps a portion of the fish stocked upstream passively dispersed downstream but when experiencing warmer temperatures, returned to where they previously experienced colder water. If a similar proportion of fish stocked downstream passively dispersed downstream during the summer, they would have quickly reached a section of the river where temperatures were lethal. Thus, the direction in which a fish disperses may be a tradeoff between previous experience and the instinct to thermoregulate, with the general tendency of stocked fish to disperse downstream. We do not claim to provide any support for this hypothesis from the results presented here, but such hypotheses can provide a basis for future research.

Management Implications

Our findings add to the growing body of literature demonstrating the negative relationship between urbanization and stream water temperature (Bartholow

1991; LeBlanc et al. 1997; Paul and Meyer 2001; Wang et al. 2003; Krause et al. 2004) and strongly suggest that urbanization increases mortality in rainbow trout. Increased water temperatures result in decreases in angler success and satisfaction, even at temperatures lower (as low as 19°C; McMichael and Kaya 1991) than we observed in the downstream reaches during the summer. Traditionally, the best physical habitat for trout (e.g., shoals) occurred in the downstream reaches of the Chattahoochee River (Nestler et al. 1984), and correspondingly, that area experienced the most angler effort (Martin 1985a, 1985b). Unfortunately, expected increases in urbanization and water use will probably result in even greater loses in trout angling opportunities on the Chattahoochee River unless effective water temperature management plans can be developed.

We also found that releases from Buford Dam (or lack thereof) significantly influence summer temperatures in the Chattahoochee River between Atlanta and Lake Lanier (the lake created by Buford Dam). This suggests that water temperatures can be managed by controlling the rate at which water is released from an upstream dam. For example, we estimate that for every 100 m^3 of water released each day during the summer, 53 fewer exceedance intervals occur per month (Table 6). Such a management strategy would require the consideration of other values that serve society at large, such as power generation, recreation on Lake Lanier, and municipal water supplies, in addition to the rainbow trout fishery. Thus, the development of effective strategies will be complicated by the complexity and uncertainty associated with the response of the fishery and the consideration of multiple and competing objectives. Decision analysis is a valuable tool for developing and evaluating management strategies under uncertainty (e.g., Peterson and Evans 2003) and would be a useful next step toward managing the trout fishery in the Chattahoochee River.

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