FORAGE REQUIREMENTS OF BROWN TROUT IN LAKE JOCASSEE

STUDY COMPLETION REPORT

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Study Title: FORAGE REQUIREMENTS OF BROWN TROUT IN LAKE JOCASSEE

Period Covered July 2008 - June 2010

Summary

1) Population data for Lake Jocassee indicated that a small percentage of the stocked fish survived to enter the fishery (5%) and that recent annual survival of harvestable fish was low (12%). There is substantial uncertainty in these estimates.

2) Relative condition of brown trout in Lake Jocassee varied seasonally. During middle (1989-2002) and recent (2003-2008) years, condition in May was consistently high. Condition in November was consistently lower, with the decline more severe during recent years.

3) A bioenergetic model using a 10-18 ºC temperature annual range and feeding rate parameter P=0.55 provided a plausible fit to growth data from marked cohorts of brown trout in Lake Jocassee during their first year in the lake. Nine survival scenarios were run. Survival to harvestable size was set at 5, 15, or 25%, and annual survival of harvestable fish was set at 10, 30, or 50%. Scenario 1 (VERY LOW survival; 5% survival to harvestable size, 10% annual survival) represents the current population in Lake Jocassee. Forage requirements were simulated for winter (mid-November to mid-March), spring-early summer (mid-March to mid-July), and late summer-fall (mid-July to mid-November) seasons for a population with initial size and numbers of stocked fish based on data for Lake Jocassee. The prey requirement was converted from biomass to numbers of fish for comparison with forage populations in Lake Jocassee.

4) Field data from Lake Jocassee, combined with simulation results from the VERY LOW survival scenario, give a picture of a population that experiences a short season of abundant forage in spring and, possibly, early summer. During late summer-fall, forage is abundant, but thermal

stratification limits access by the trout. During the winter season, forage is initially abundant, but becomes depleted, due in part to predation by the trout. The level of depletion appears to prevent improvement in condition over the winter, although it does not severely curtail growth.

5) The simulated winter forage requirement (1.9 million fish) in the VERY LOW survival scenario was equal to about half of the median number of forage fish in Lake Jocassee during winter (hydroacoustic survey data for 1989-2005). It exceeded the winter forage population in 2 of 17 years. The simulated requirement could account for a substantial portion of the typical winter decline in forage fish (median decline of 2.6 million fish in 1989-2005).

6) The forage in Lake Jocassee appears to have limited capacity to support improvement in the brown trout fishery. At the current harvest level of brown trout, the winter forage population cannot sustain substantially higher survival to harvestable size, whether this is achieved by stocking at a higher level or by improving survival at the current stocking level. The winter forage population can sustain a reduced harvest rate of brown trout that would substantially increase the average size of a harvested fish.

7) Recent data suggest that approximately 1 of 20 stocked fish is attaining harvestable size. Future study is needed to define the immediate fate of stocked fish. Because available forage seems adequate, predation, illegal harvest, catch-and-release mortality of deep-caught trout,or failure to adapt to the wild are possible explanations.

Introduction

Lake Jocassee supports a valuable sport fishery for brown trout (*Salmo trutta*). The fishery was established in the1970s. Annual harvest was greatest (2,000-8,000 fish) during the first decade (Figure 1). The annual harvest dropped in 1989, and minimum size for harvestable fish was raised to 15 inches from 12 inches in 1991. Except for a few years of higher harvests in 2000-2002, the median harvest since 1989 has been near 1,000 fish annually.

The size of harvested fish increased sharply after the minimum limit was raised (Figure 1). More recently, the size of harvested fish has decreased: mean weights in 2000-2005 differed significantly from mean weights in 1993-1999 (two-sample t test, p=0.005). Fall condition has also declined in recent years (Figure 2). Analysis of variance showed that November means differed between the early (1977-1982) and recent (2003-2008) time periods and between the middle (1989-2002) and recent time periods (simultaneous comparisons by Tukey method). Spring condition, however, did not differ among these time periods.

The forage base for brown trout in Lake Jocassee consists mainly of blueback herring (*Alosa aestivalis*) and threadfin shad (*Dorosoma petenense*). Small (<40-50 cm) brown trout in Lake Jocassee consume more threadfin shad; large brown trout consume more blueback herring (D. Rankin, pers. comm.). Among the other major piscivores in Lake Jocassee, rainbow trout (*Onchorhynchus mykiss*) and redeye bass (*Micropterus coosae*) are believed to feed extensively on blueback herring and threadfin shad.

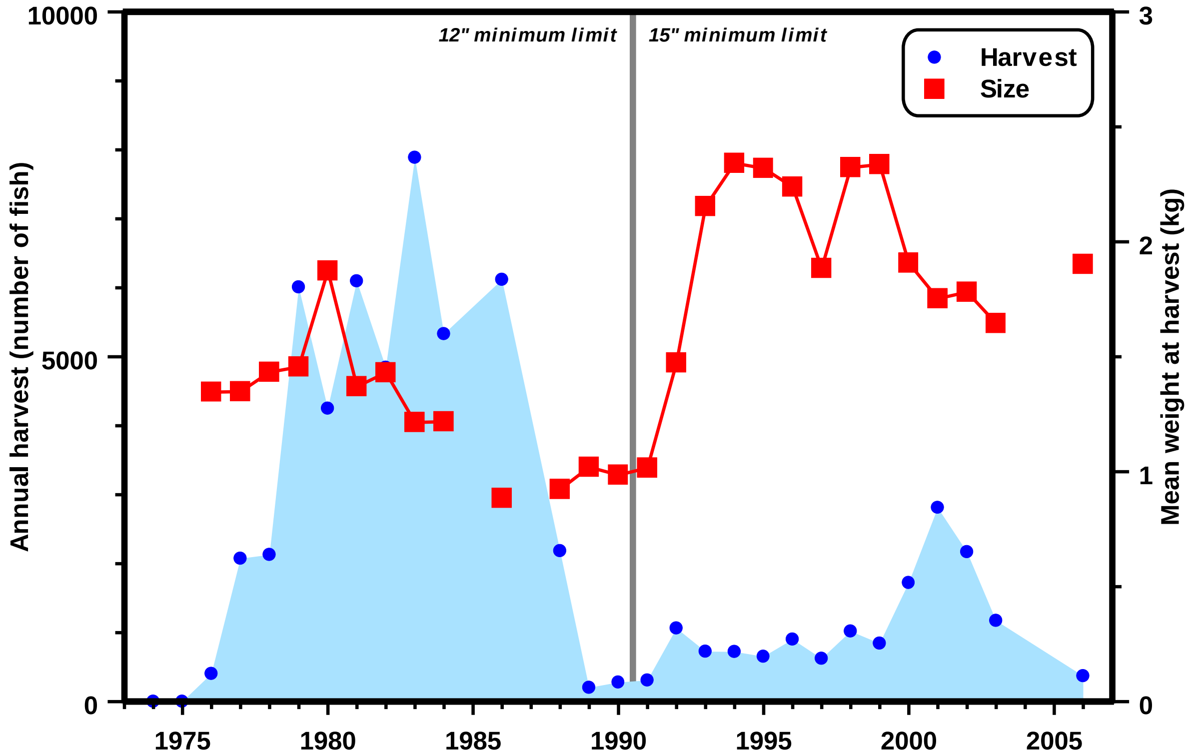

Figure 1. Harvest of brown trout at Lake Jocassee, 1974-2006. Estimates from creel surveys were provided by Dan Rankin (SC DNR). Note the change in size limit, implemented in 1991.

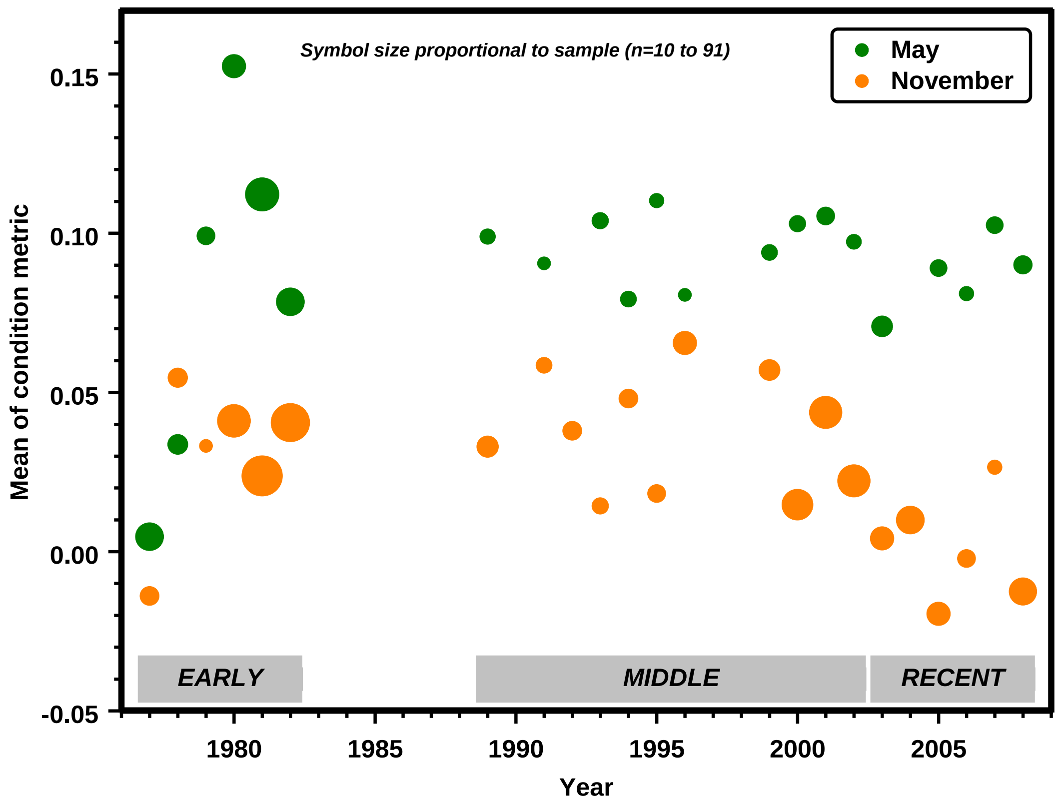

Figure 2. Condition of brown trout in Lake Jocassee, 1977-2008. Brown trout were collected by gill netting. Condition metric is defined below. Fish <300 g and condition values more extreme than ±0.4 were excluded from computation of means. Means with <10 fish were excluded from plot and analysis. The breakpoint between the middle and recent time periods maximizes the difference between the two groups of years. Data were provided by D. Rankin (SC DNR).

Wide year-to-year fluctuations in the populations of forage fish (Rodriguez, 2010), along with the variations in the harvest and conditions of brown trout, raised questions about the potential for food limitation in the brown trout population. To investigate the adequacy of the forage base, we estimate forage requirements using a cohort-structured, bioenergetics-based population model. The feeding rate parameter in the model is adjusted to fit simulated growth to data from marked cohorts stocked in Lake Jocassee. The first among nine simulated survival scenarios is based on estimates from data for the Lake Jocassee population. Additional scenarios explore the impact of higher survival on population dynamics and forage requirements. We compare simulated forage requirements of brown trout with long-term data on abundances of forage fish. We evaluate the potential for food limitation by season, considering thermal stratification of the lake and growth and condition of the brown trout, as well as the forage base.

Materials and Methods

Lake Jocassee

Lake Jocassee is a 3,063-ha impoundment in western South Carolina in the upper reaches of the Savannah River drainage. Constructed by Duke Power, it reached full pool in 1973. Lake Jocassee serves as the upper pool for the 610-MW Jocassee Pumped Storage Station and as the lower pool for the 1,065-MW Bad Creek Pumped Storage Station.

The reservoir is deep and oligomictic. Maximum depth at full pool (338.3 m above mean sea level) is 107 m; mean depth is 46 m (Barwick et al., 2004). Surface temperatures range annually from ~10 ºC in February to ~27 ºC in August (Figure 3). In the deeper parts of the reservoir, water temperature remains near 10 ºC throughout the year. The reservoir mixes completely in about 40% of years (W. Foris, Duke Power, unpublished data). Following winters without mixing, dissolved oxygen becomes depleted in the hypolimnion. By September, the zone of dissolved oxygen <5 mg/liter may extend 40-50 m up from the bottom of the lake.

The reservoir is also oligotrophic: nutrients and productivity are low. Water chemistry data for five SC DHEC monitoring stations in 1999-2006 were obtained from the EPA (STORET database). Alkalinity was low, typically 5-6 mg/liter, and pH was circumneutral, typically 5.7-7.3). Total phosphorus rarely exceeded the detection limit of 0.02 mg/liter; the maximum was 0.04 mg/liter. Total nitrogen was typically 0.03-0.25 mg/liter; the maximum was 0.7 mg/liter. Consistent with these low nutrient concentrations, summer chlorophyll values were typically 1-2 micrograms/liters (2002 and 2005 only, 4 stations); the maximum was 6.5 micrograms/liter. Nutrients and chlorophyll met the applicable water standards (SC DHEC, 20004: total phosphorus $\leq$ 0.2 mg/liter; total nitrogen $\leq$ 0.35 mg/liter; chlorophyll a $\leq$ 10 micrograms/liter). The waters of Lake Jocassee are listed as impaired only for excessive mercury concentrations (SC DHEC, 2006).

Brown Trout in Lake Jocassee

Distribution

For brown trout in southeastern reservoirs, water with temperature $\leq$ 20 °C and dissolved oxygen $\geq$ 5 mg/liter generally provides suitable habitat (Barwick, Foltz, and Rankin, 2004) . During winter and most of spring (December through April), the entire water column of Lake Jocassee is thermally suitable for brown trout (Figure 3), although dissolved oxygen may be insufficient in deeper parts of the lake. As the epilimnion continues to warm during summer, trout are limited to increasingly greater depths.

During a summer study of habitat preferences in Lake Jocassee, brown trout implanted with transmitters ranged over depths from 14-15 m to 54-55 m (Barwick et al., 2004; 14 individuals, 190

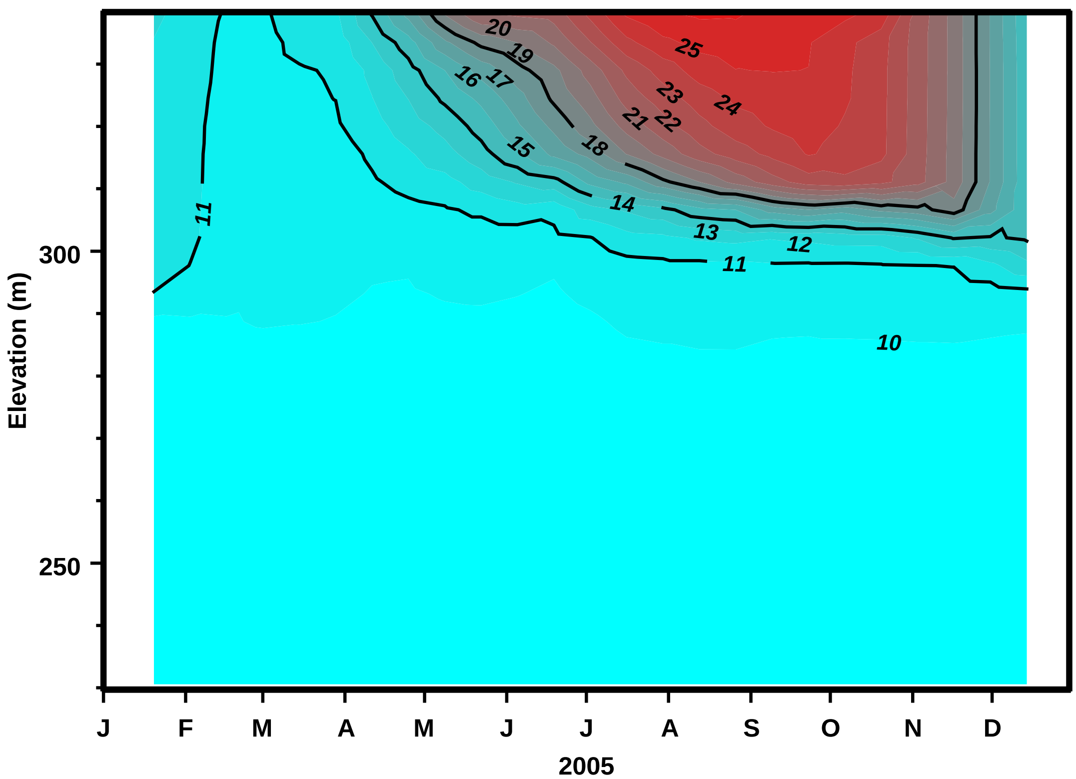

Figure 3. Depth-time plot of water temperature in Lake Jocassee, 2005. Monthly profiles of temperature at station 558.0 were provided by Duke Power. Isotherms marked with lines are used as thermal upper limits in bioenergetic models described below. The lake did not mix completely in winter of 2005.

observations). The fish were 0.8-3.6 kg in weight, but more than 95% of the observations came from fish of 1.3 kg or more. Reported temperatures were 9-21 ˚C. Distributions of the fish were bimodal in July (12 fish; modes: 14-14.9 ˚C and 18-19 m; 11-11.9 ˚C and 24-25 m) and August (13 fish; 17-17.9 ˚C and 22-23 m; 10-10.9 ˚C and 26-27 m), but unimodal in September (6 fish; 10-10.9 ˚C and 36–37 m).

Stocking and management

The brown trout fishery at Lake Jocassee is a put-grow-and take fishery. Natural reproduction is negligible.

The stocking program began in 1973, the year in which construction of the lake was completed (Figure 4). Brown trout have been stocked in fall (usually December) at age 1, in spring (usually February or March) at age 1^+, and in fall (usually November or December) at age 2. Length at stocking depends on age and culture conditions: reported ranges for fish of age $1\text{-}1^+$ were typically 7-8 or 8-9 inches; for fish of age 2, 10-11 inches. Under the current stocking program, 25,000 fish of age 2 are stocked in fall.

To estimate yield, we compared the number stocked with the number harvested in the year that the stocked fish reached harvestable size. Brown trout stocked in fall at age 1 or spring at age 1^+ reach harvestable size (15 inches under the current regulations) by the following fall; brown trout stocked in fall at age 2 reach this size by the following spring or summer. The harvest is typically dominated by fish stocked in the previous year. We assumed that the contributions of earlier stocks would be equivalent to that stock's contribution to later harvests.

Since the 15-inch limit was implemented in 1991, the median yield of brown trout, based on creel survey data, has been 2% of the number stocked (Figure 4; range 1-5%, n=14 years). The most recent estimate (2005 stock; 2006 creel survey) was 1%, and the corresponding return to creel by weight was 11%. Estimates of yield since the current stocking program was implemented are not yet available.

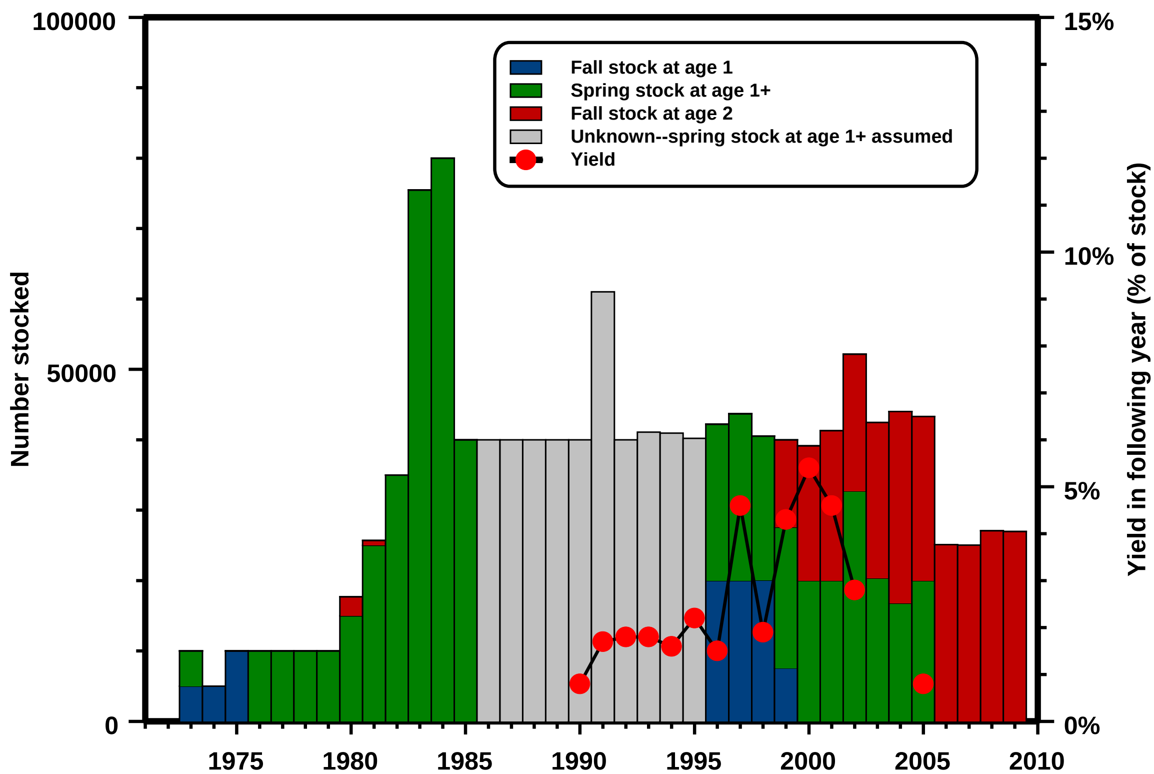

Figure 4. Stocking and yield of brown trout at Lake Jocassee, 1973-2009. Yield is shown for fish stocked in 1990 and later; these cohorts were harvested after the 15-inch minimum size limit was implemented. Note that fish stocked in fall at age 1 are assumed to reach harvestable size in the same year as fish stocked in the following spring. Data were provided by D. Rankin (SC DNR).

Recent growth and condition

Brown trout were measured at the time of stocking in 2006 and 2007 (Table 1, Figure 5). The trout stocked in 2007 were slightly larger than those stocked in 2006. Estimated mean weights of the individual stocked fish were 193 g (range 82-316 g) in 2006 and 220 g (range 88-373 g) in 2007.

All of the stocked trout were marked with a finclip (adipose fin in 2006; right pelvic fin in 2007). Subsequent sampling included gillnetting (10 or more net nights in fall, winter, and spring) and a creel survey in 2008.

The 2006 and 2007 cohorts showed similar patterns of growth during their first year in the lake (Figure 6). Growth was most rapid during the six months after stocking. Samples during this period were sparse, but suggest that growth may have accelerated after March. Growth slowed during summer. Samples were too sparse to evaluate seasonal growth rates of fish after their first year in the lake.

Growth of the recent cohorts differed substantially from growth of the well-sampled 1981 cohort (Figure 6). The 1981 cohort, stocked at age 1.5, attained a median weight of 2.5 kg by age 3, about a year sooner that the 2006 cohort. The 2006 and 2007 cohorts were about half this weight at age 3.

We measured condition as the difference between observed $\log_{10}$(weight in g) and predicted $\log_{10}$(weight). The prediction was generated using a regression of $\log_{10}$(weight) against $\log_{10}$(length in mm) for the March data (2006 and 2007 combined). We used the March data for the regression because the range of lengths was wide, all of the fish had been in the lake for at least 4 months, and the fit was excellent (r^2=0.98, n=19).

Table 1. Size of brown trout stocked into Lake Jocassee, 2006-2007. Weight was estimated using the equation log10 (mass in pounds) = 3.00809 log10 (length in inches) – 3.37430, which was developed for brown trout (lake form) in Michigan (Schneider, Laarman, and Gowing, 2000). Data were provided by D. Rankin (SC DNR).

	2006 (n=100)		***2007 (n=99)***	
Metric	***Length (mm)***	***Weight (g)***	***Length (mm)***	***Weight (g)***
Minimum	190	82	195	88
5th percentile	223	132	230	145
Mean	252	193	263	220
Median	254	195	264	219
95th percentile	276	251	291	294
Maximum	298	316	315	373

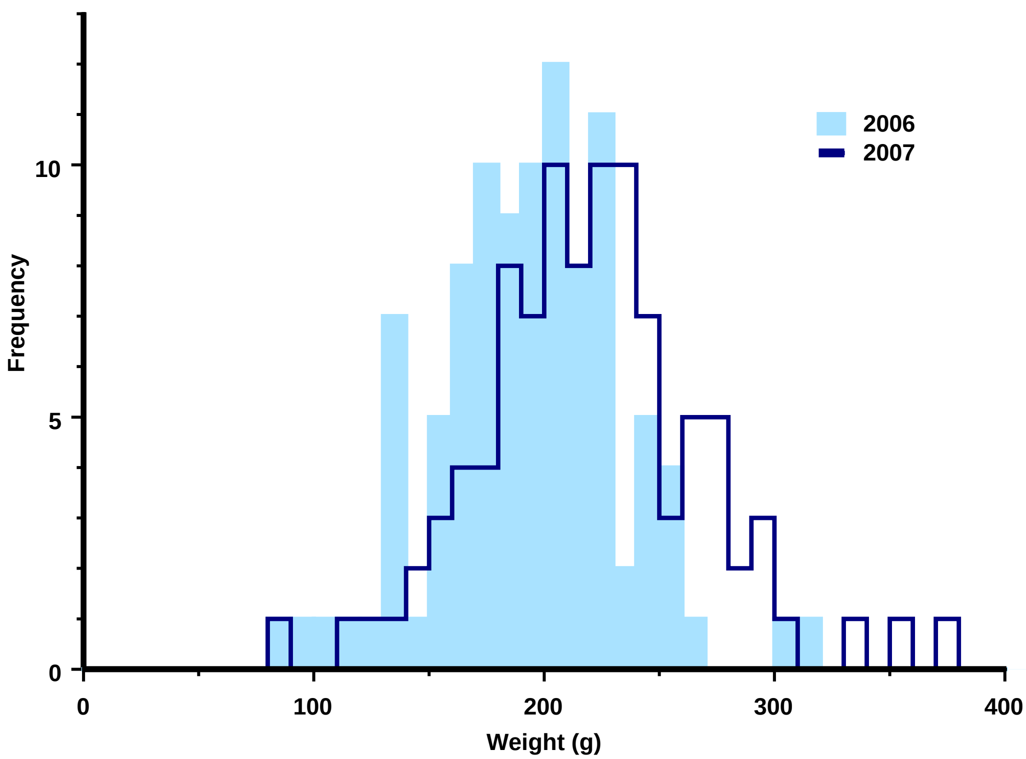

Figure 5. Size of brown trout stocked into Lake Jocassee, 2006-2007.

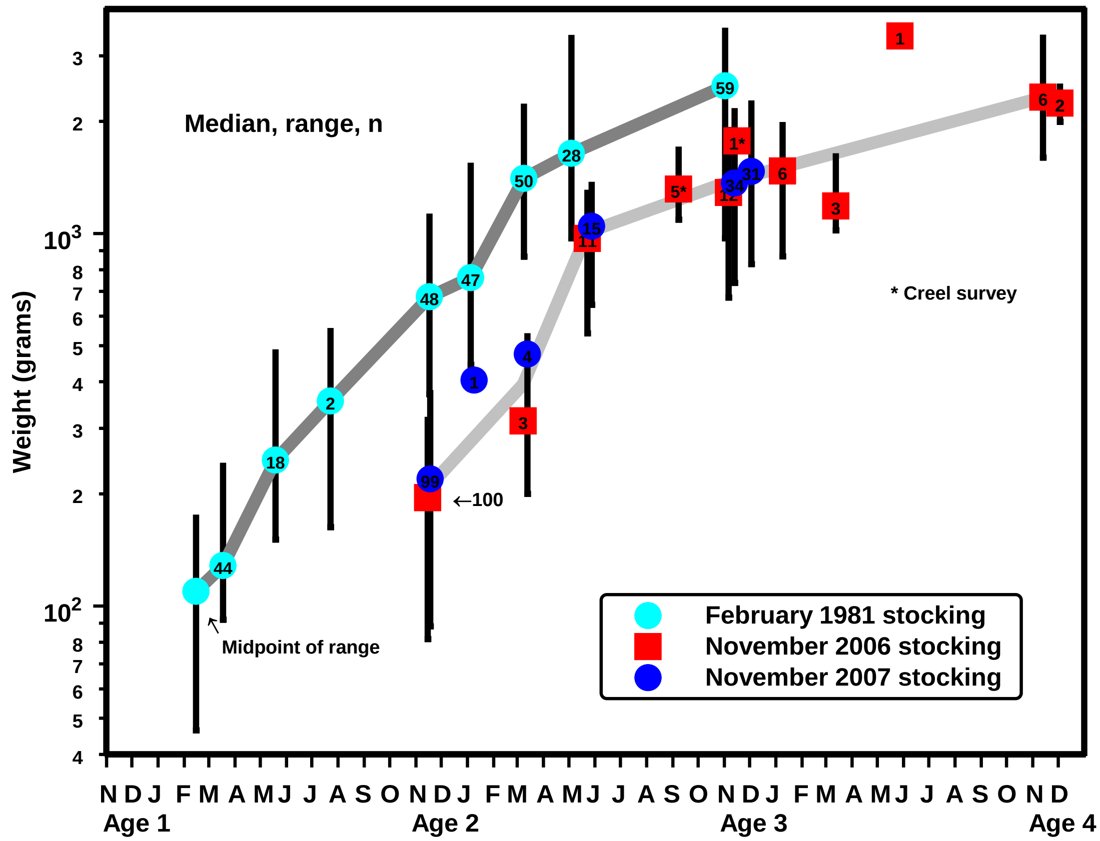

Figure 6. Growth of marked cohorts of brown trout in Lake Jocassee. Initial sizes were measured at time of stocking (Table 1, Figure 1); subsequent measurements were made on fish from gill net samples or creel surveys. Slopes of the lines are proportional to growth rates per unit weight. Statistics were not adjusted for net selectivity, so the medians may be biased. Data for second-year growth of the 2007 cohort were not yet available. All data were provided by D. Rankin (SC DNR).

Condition in May differed significantly from condition in the preceding March and following November samples (Figure 7). Other pairs of samples did not differ (simultaneous confidence intervals by Tukey method). Slowed growth of the age 2 fish in the summer and fall after stocking coincided with the annual deterioration of condition between May and November.

Survival

Because no direct estimates were available, we estimated survival of trout from the time of stocking to the time of attaining harvestable size indirectly. We subdivided the population into two size classes, based on whether or not the fish had grown to harvestable size. If the number of fish stocked and their survival rates are similar from one year to the next, the number of recruits to the harvestable size class in a year will be about the same as the number of deaths in the harvestable size class (Figure 8).

The creel census should estimate the number of deaths due to harvest annually. If the number of deaths due to causes other than harvest were small, the creel census would slightly underestimate the total number of deaths, as well as the number of recruits. However, the creel census does not include the night fishery, which is believed to be substantial (D. Rankin, SC DNR). Mortality of fish caught but released may also be substantial.

Based on creel surveys for years since the 15-inch size limit was imposed, the median harvest was equal to 2% of the number stocked in the previous year (Figure 4). Allowing for natural mortality, catch-and-release mortality, and underestimates of the harvest, we estimate that about 5% of stocked fish survive to harvestable size.

Annual survival appears also appears to be low for fish of harvestable size. Gill netting in November and December 2008 (25 net nights in five locations) yielded 81 brown trout, including 66 marked brown trout from the 2007 cohort and 8 marked brown trout from the 2006 cohort. These

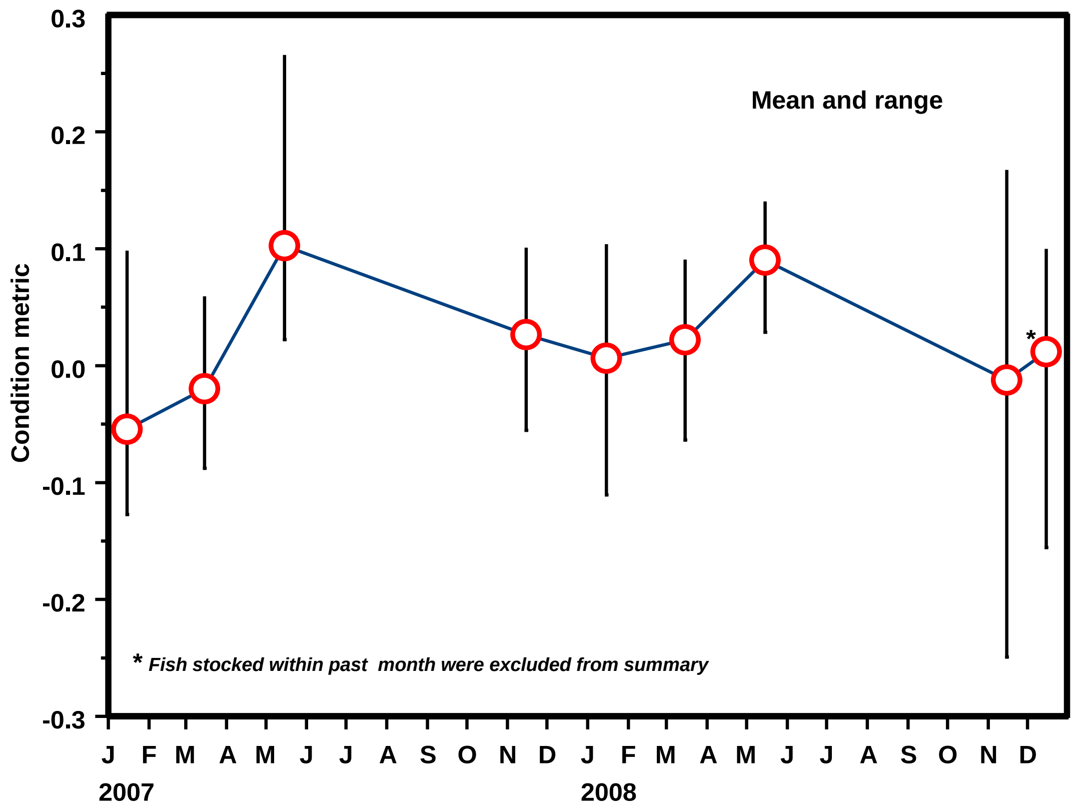

Figure 7. Condition of brown trout in Lake Jocassee, 2007-2008. Condition metric is described in text; a higher value indicates better condition. To eliminate recently stocked fish from analysis, fish <300 g were excluded. Fish stocked within past month in December 2008 sample were identified by weight <350 g. Number of fish in sample ranged from 9 to 43. Condition in May of each year differed significantly from condition in the preceding March and following November samples, but other pairs of samples did not differ (simultaneous confidence intervals by Tukey method). Data for analysis were provided by D. Rankin (SC DNR).

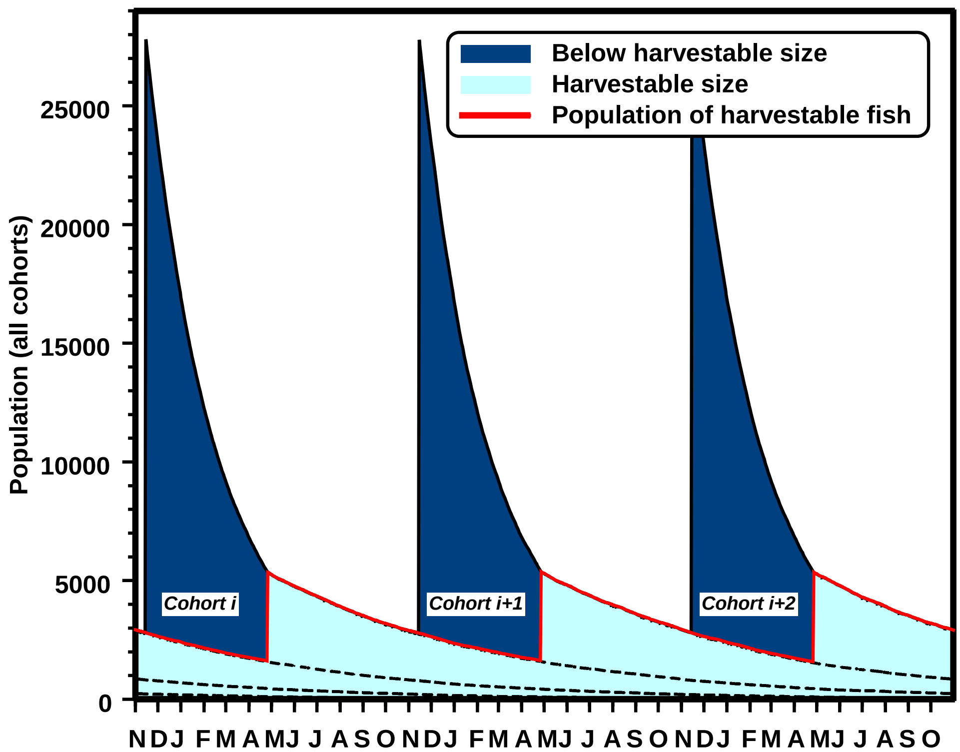

Figure 8. Simulated dynamics of a cohort-structured population. Number of fish stocked, growth rate, survival from stocking to attainment of harvestable size, and annual survival of harvestable size were consistent from year to year. This example was simulated with Scenario 5 (described below); cohorts approach extinction five years after stocking.

numbers yield an annual survival over the second year in the lake of 12% (95% confidence interval estimate: 5 to 20%). All of these fish had attained harvestable size, based on measured lengths. The data were not adjusted for selectivity of the nets, and the analysis assumes that fish from two cohorts were caught with equal efficiency.

We computed annual survival from catch curves for two earlier marked cohorts. The 1974 year class, stocked in December 1975, had 21% annual survival from age 3 (in November of sample year) to age 6 (r^2=0.999). The 1976 year class, stocked in January 1978, had 45% annual survival from age 3 to age 5 (r^2=0.87). January, March, May, and November samples were combined. Fish of age 2 were omitted, because they appear to be underrepresented in the first 4-6 months following stocking. (Fish stocked at age 2 in fall also appear to be underrepresented in samples taken during the first 4-6 months following stocking.) Numbers based on November samples only were too small for analysis. None of the other longitudinal series appeared to be suitable for catch curve analysis; evidently, very few trout survive past age 3.

Abundance of forage

Stocks of forage fish are routinely assessed in November and March by hydroacoustic sampling by Duke Power. Additionally, in November, the species and size composition are determined from purse seine samples by Duke Power. For 1989-2005, the median combined population of threadfin shad and blueback herring for Lake Jocassee was 4 million fish in November and 1 million fish in March (Figure 9). The median difference between populations in the fall and the following spring was 1.2 million fish (range 1.2-10.3 million, n=15 years). The median average weight for the combined population in November 2000-2005 was 5.6 g, and median standing stock was 20 metric tons (Table 2).

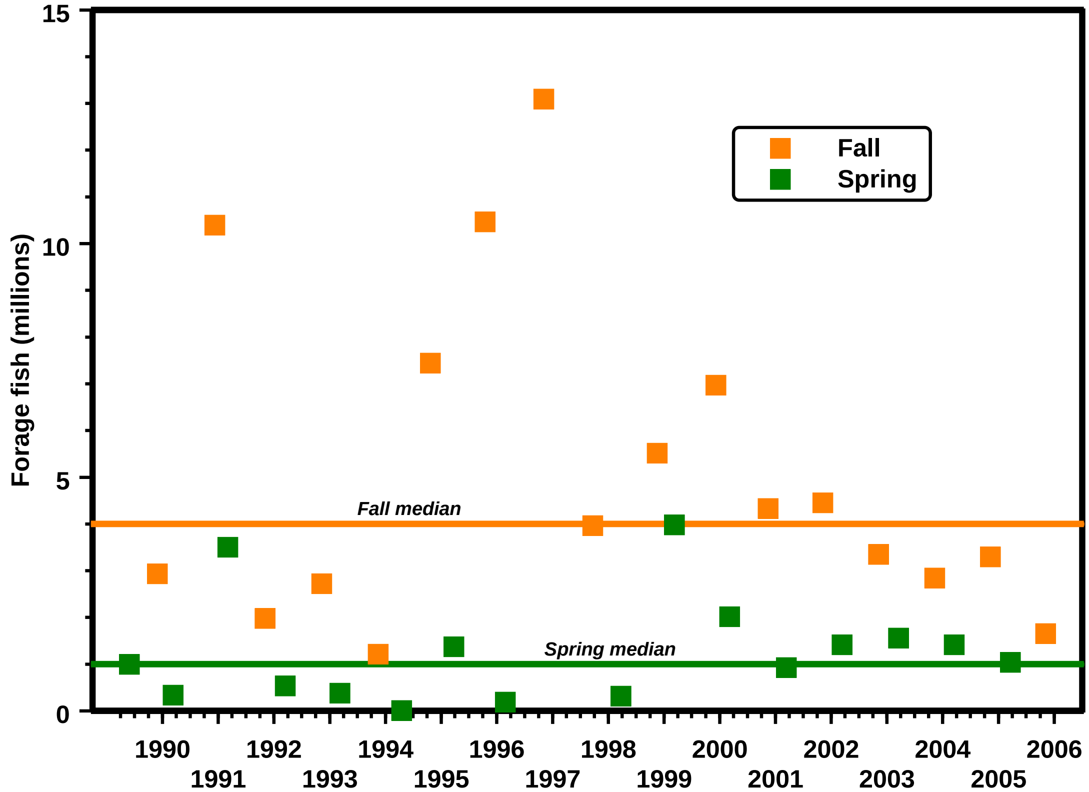

Figure 9. Spring and fall abundances of forage fish in Lake Jocassee, 1989-2005. Hydroacoustic survey data were provided by D. Coughlan (Duke Power).

Table 2. November standing stock of forage fish in Lake Jocasssee, 2000-2005. Population estimate is based on hydroacoustic survey; composition and mean weight are based on purse seine catch. Blueback herring were separated by size class in 2001 and 2002 only. Data were provided by D. Coughlan (Duke Power).

Year	*Population (millions)*	*Species*	*Composition*	*Mean weight (g)*	*Standing stock (metric tons)*
2000	4.3	All		4.3	18.6
		Threadfin shad	73%	2.6	8.1
		Blueback herring	27%	9.0	10.5
2001	4.5	All		5.2	23.0
		Threadfin shad	32%	2.3	3.2
		Blueback herring (<120 mm)	55%	3.2	7.8
		Blueback herring (>120 mm)	13%	21.1	12.0
2002	3.3	All		6.0	20.0
		Threadfin shad	48%	2.9	4.7
		Blueback herring (<120 mm)	32%	4.0	4.2
		Blueback herring (>120 mm)	20%	16.5	11.1
2003	2.8	All		3.7	10.5
		Threadfin shad	24%	3.4	2.3
		Blueback herring	76%	3.8	8.2
2004	3.3	All		7.6	25.0
		Threadfin shad	24%	4.3	3.4
		Blueback herring	76%	8.7	21.7
2005	1.7	All		8.4	13.8
		Threadfin shad	31%	4.8	2.5
		Blueback herring	69%	10.0	11.4

Similar assessments of forage fish by Duke Power in Lake Norman provide information about growth in a similar system. Lake Norman is a large oligotrophic reservoir in the Piedmont region of North Carolina (Buetow, 2008). Forage fish were collected by purse seining in July, September, and December of 2002. Average weights of threadfin shad and alewife, respectively, were 0.6 g and 1.4 g in July, 1.0 g and 3.4 g in September, and 2.3 g and 4.5 g in December. For both species, average weight approximately tripled from July to November (interpolated).

Brown Trout Population Model

To estimate forage requirements of the brown trout population, we built a cohort-structured model, assuming similar size at stocking and subsequent growth for all members of the cohort. The simulations were written in S-Plus (Insightful Corporation, Seattle, WA; code available from BET). The functions describing growth and forage requirements for an individual fish were adapted from the bioenergetics model by Dieterman et al. (2004).

In the simulations, an initial population and body size at time of stocking are specified. Bionenergetic functions, which depend on water temperature and a feeding rate parameter, determine subsequent growth in body size. Survival depends on whether cohort has attained harvestable size.

Bioenergetics

Bioenergetic models for brown trout have been developed for a variety of applications (Van Winkle et al., 1998; Elliott and Hurley, 1999; Hayes, Stark, and Shearer, 2001; Brown, 2004; Dieterman, Thorn, and Anderson, 2004). Dieterman et al. (2004) modeled brown trout in Minnesota streams using Fish Bioenergetics 3.0 (University of Wisconsin, Madison, WI). Negus et al. (2004) subsequently applied this model to brown trout in Lake Superior.

For the brown trout population in Lake Jocassee, we used bioenergetics equations from Fish Bioeenergetics 3.0 with parameters from Dieterman et al. (Table 3). We set prey energy density at 5,000 joules/g wet mass. This value lies near the middle of the range of values compiled for prey fishes by Hanson et al. (1997, Appendix B) and Negus et al. (2004, Table 12).

Processes considered in the Fish Bioenergetics 3.0 model are energy gains due to consumption and energy losses due respiration and waste, including egestion, excretion, and the cost of assimilation (specific dynamic action). The difference between consumption and waste is the net consumption. Net consumption is about 60% of total consumption. The difference between net consumption and respiration is available for allocation to growth or reproduction. These processes depend on water temperature, body mass of the fish, and the feeding rate parameter P.

With the feeding rate parameter set at P=1, consumption for a 1,000 g fish reaches a maximum at 17˚C; growth reaches a maximum at 14 ˚C (Figure 10). At P=0.5, co nsumption reaches a maximum at 17 ˚C; growth, at 12 ˚C. The break-even point, where net consumption equals respiration, occurs at just under 20˚C at P=1. Reducing P slows growth and shifts the growth maximum and break-even point to lower temperatures. Growth and consumption are higher for smaller fish, and lower for larger fish, but the maxima and break-even points occur at similar temperatures (model results not shown). Between ~10-16 ˚C, depending on P, the response of net growth to temperature is fairly flat.

When Lake Jocassee is unstratified, or weakly stratified, from January to April, surface temperature is a good estimate of the temperature experienced by brown trout. However, as discussed above, brown trout experience a range of temperatures when the lake is stratified. Individuals differ in thermal preferences, and the typical condition for the population is not well-

Table 3. Parameter values for bioenergetics functions. Equation numbers refer to Hanson et al. (1997); parameters were taken from Dieterman et al. (2004).

Process	***Parameter***	***Value***
Consumption (eq. 3)	CA	0.2161
	CB	-0.233
	CQ	3.8
	CTO	17.5
	CTM	17.5
	CTL	20.8
	CK1	0.23
	CK4	0.10
Respiration (eq. 1)	RA	0.0013
	RB	-0.269
	RQ	0.0938
	RTO	0.0234
	RTM	0
	RTL	25
	RK1	1
	RK4	0.13
	ACT	9.7
	BACT	0.0405
	SDA	0.172
Egestion/excretion (eq. 3)	FA	0.212
	FB	-0.222
	FG	0.631
	UA	0.0314
	UB	0.58
	UG	-0.299
Predator energy density (eq. 2)	Alpha 1	5591
	Beta 1	7.7183
	Cutoff	151
	Alpha 2	6582
	Beta 2	1.1246

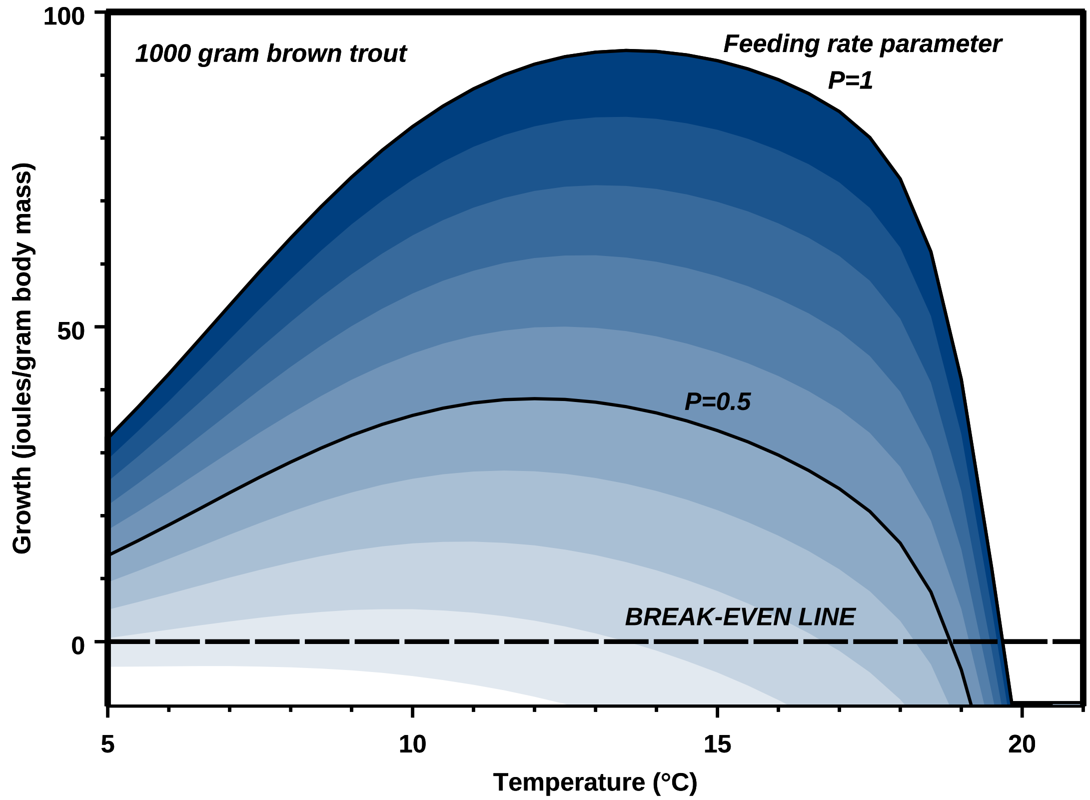

Figure 10. Growth of brown trout, as described by bioenergetics functions. Results are shown for a 1000-gram fish. Net consumption equals respiration at points along the break-even line.

specified. We constructed alternative functions to bracket a plausible range of thermal conditions. These functions are all based on sine curves fitted to surface temperature (Figure 11)

The first function assumes that the fish select the warmest temperature available in the lake, up to 18 ˚C, near the upper of the two temperature modes in observed in July (Barwick et al., 2004). The second function assumes that the fish select the warmest temperature, up to 14˚C, near the upper of the two modes in August. The third function assumes that the fish select the warmest temperature, up to 11˚C, near the lower modes in July and August and near the single mode in September. The three temperature functions have annual ranges of 10-18 ˚C, 10-14 ˚C, and 10-11 ˚C. Corresponding limits to vertical distributions in the lake are shown by the highlighted isotherms in Figure 3.

To estimate the feeding rate parameter P, we fitted simulated growth to observed growth of fish stocked in 2006 and 2007 (Figure 12) for each of the three temperature functions. Initial sizes in the simulations were 80, 130, 300, and 380 g. These values bracket the ranges and the 5^{th} and 95^{th} percentiles of the estimated weights of stocked trout in 2006 and 2007 (see Table 1, Figure 5).

P values were fitted to the nearest 0.05 unit to growth during the first year after stocking (Figure 12). The simulations reproduced both the medians and the ranges of sizes of fish at age 3 (in November; 47 observations); size at age 2.5 (in May; 27 observations) was underestimated. Simulations during the second year after stocking overestimated the November medians. The number of observations seemed too small (6 observations in November; 9 observations for the entire year) and the values to variable to support fitting a separate P value. The effect of reducing P after the first year is examined in the sensitivity analysis below.

To prevent fish from attaining unrealistically large sizes, we applied a logistic function with maximum of 8,000 g to curtail growth of fish between 4,000 and 8,000 g in weight. (The record

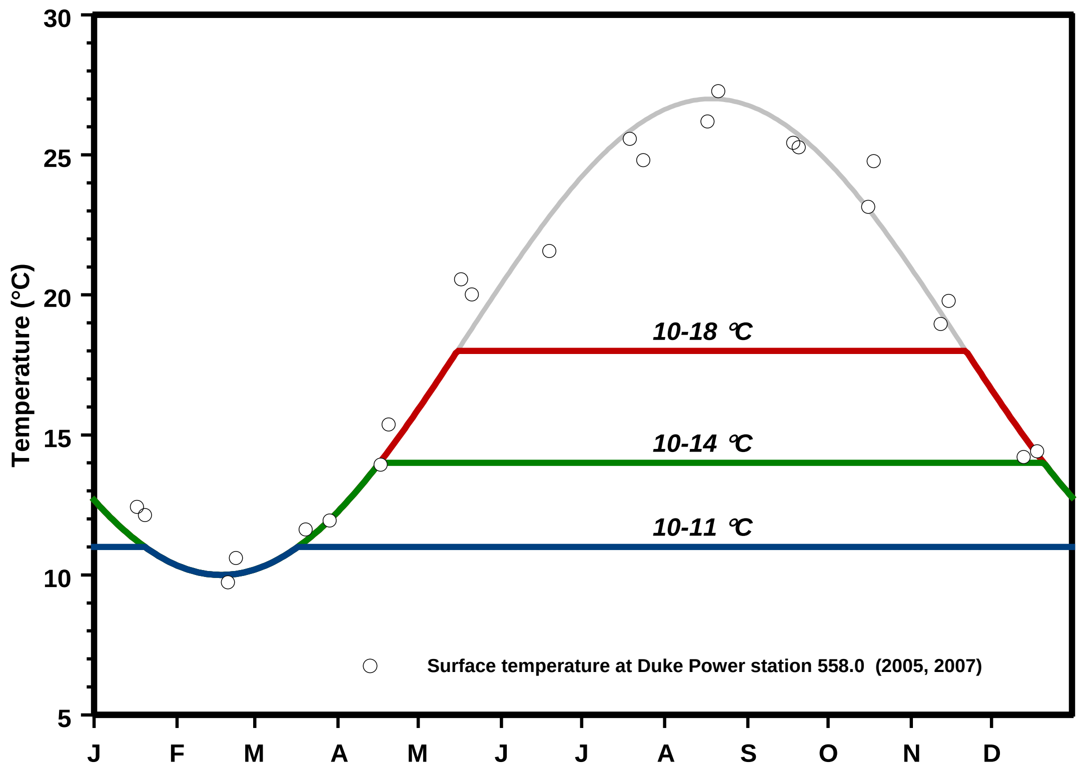

Figure 11. Annual temperature functions. Sine function was fitted to surface temperatures at Duke Power station 558.0 (data provided by Duke Power).

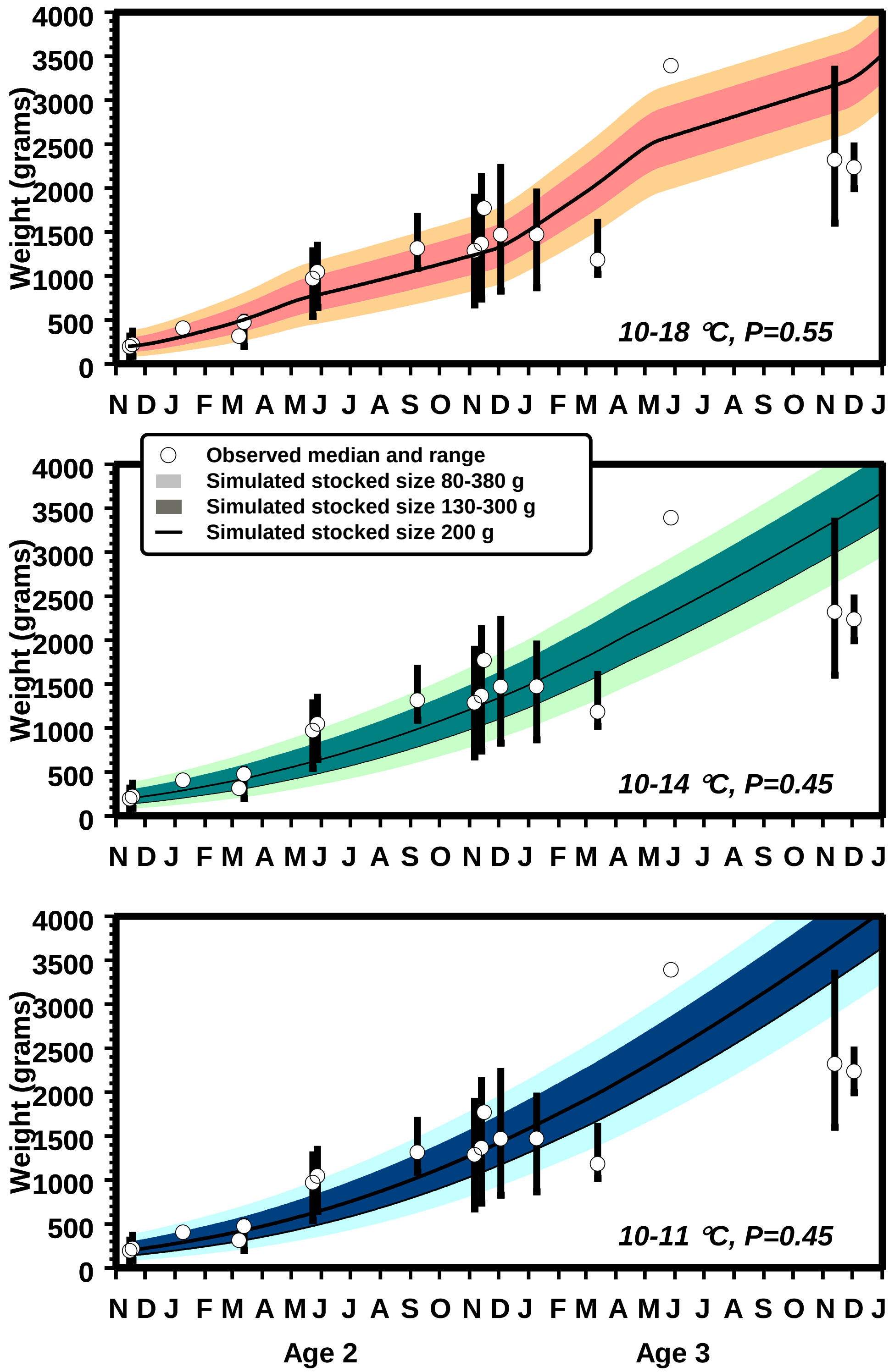

Figure 12. Simulated and observed growth of brown trout in Lake Jocassee. Fish were stocked at age 2. Simulated growth is shown for fish of 80-380 g (outer range) and 130-300 g (inner range) at stocking. Observed growth is shown for cohorts stocked in 2006 and 2007 (Figure 3).

weight for a brown trout from Lake Jocassee is 7.98 kg.) In simulations with the 10-18 ˚C annual temperature function and stocking at age 2 at 200 g, this logistic limitation began at age 4.25 (2.25 years after stocking). A size of 7,000 g was attained at age 6.5 (4.5 years after stocking). Subsequent growth was slow to negligible.

Simulations with the 10-18 ˚C annual temperature function and P=0.55 produced slower growth in summer than in cooler seasons. Simulations with the 10-14 ˚C function and P=0.45 and with 10-11 ˚C function and P=0.45 gave similar results, consistent with the flat response of growth to temperature in the range 10-14 ˚C for P in the range of 0.4-0.5 (Figure 10).

The time of attaining harvestable size (15 in, equivalent to 685 g) ranged from mid-February for a fish of 380 g at stocking in mid-November to mid-September for a fish of 80 g at stocking with the 10-18 ˚C annual temperature function. Corresponding ranges were early March to late September or early October for other two temperature functions.

Population dynamics

Initial populations for the cohorts were set at 25,000 fish stocked in mid-November at age 2, consistent with the current stocking program at Lake Jocassee. Unless noted otherwise, initial size was 200 g, near the median for the brown trout stocked in 2006 and 2007 (Table 1, Figure 5). The effect of size structure in the initial populations is examined in the sensitivity analysis below.

Survival rates were set depending on whether the members of the cohort were below or above the minimum size for harvest. We constructed scenarios with 5, 15, or 25% survival to harvestable size (S_1) and 10, 30, or 50% annual survival of harvestable fish (S_2). We present results in tabular form for all nine scenarios. We illustrate some results in more detail for three of the scenarios: VERY LOW (S_1=5%, S_2=10%), LOW (S_1=15%, S_2=30%), and MODERATE (S_1=25%, S_2=50%).

Survival rates in the VERY LOW scenario correspond to current estimates for the population in Lake Jocassee.

For fish below harvestable size, a daily per capita survival probability was computed from the percentage surviving to harvestable size and the number of days required to attain harvestable size. For a given percentage surviving to harvestable size, the daily survival probability thus varies with the initial size and the bioenergetic model. For fish of harvestable size, a daily per capita survival probability was computed from the annual survival probability. The population of fish was tracked in whole numbers. The number surviving each day was computed as a random binomial function of the daily survival probability.

Growth, forage requirement, and survival were computed daily for each cohort. Because the expected number of fish surviving after 10 years was small for the range of survival rates tested: (8.3 individuals out of 25,000 in the MODERATE survival scenario; 0.4 individuals in the LOW scenario; and <<1 in the VERY LOW scenario), we ended the simulations after ten years. Summary statistics were based on ten one-year age classes. For statistics such as mean weight at death, any fish alive after 10 years were included in the computations as though they had died on the last day of the simulation.

Sensitivity analyses

We tested sensitivity of the model to the temperature function in the VERY LOW, LOW, and MODERATE survival scenarios, using the annual forage requirement for a 10-cohort population as the metric. The annual forage requirement for a 10-cohort population was greatest with the 10-18 ºC annual temperature function. The alternatives did not have a substantial effect. The differences were negligible in the VERY LOW scenario, increasing to <10% in the MODERATE scenario with 10-14 ºC function and to <20% in the MODERATE scenario with the 10-11 ºC function. Because the 10-18 ºC function better represents the range of temperatures selected by marked brown trout in Lake Jocassee (Barwick et al., 2004), we chose it for the simulations. However, we note that the field study was based on fish mainly much larger than fish in age class 2 in the simulations (0.9-1.1 kg in July-September).

The annual temperature range that we chose does not reach 20 ºC, the value accepted as the upper limit for habitat suitable to brown trout in Lake Jocassee. The breakeven point for growth, as modeled, lies below 20 ºC for all values of the feeding rate parameter P. The actual location of this point for Lake Jocassee trout has not been determined.

Because the brown trout stocked into Lake Jocassee span a wide range of sizes, we examined the potential impact of size structure by subdividing the cohorts into subcohorts with different initial sizes. Again, we tested sensitivity of the model in the VERY LOW, LOW, and MODERATE survival scenarios, using the annual forage requirement for a population of 10 cohorts, initiated in 10 successive years, as the metric. We compared simulations initiated with cohorts of 25,000 200-g fish to simulations initiated with cohorts 25,000 fish divided equally among subcohorts of 157-g, 193-g, 219-g, and 254-g fish. These sizes represent the median of the combined stocking data for 2006 and 2007 (200 g) and the medians of the quartiles of the stocking data (157, 193, 219, and 254 g). The subcohorts attain harvestable size at different times, depending on initial weight. We applied the same daily survival rate to each subcohort; the value was computed to give the appropriate total reaching harvestable size from all of the subcohorts combined. The effect of size structure was not substantial. The annual forage requirement was greater by 10% or less for the simulations initiated with size-structured cohorts.

Finally, we examined the impact of reducing the feeding rate parameter P for fish after their second year in the lake. A value of P=0.45 (to the nearest 0.05 unit) gave the best fit to growth from simulated value at end of year 1 in lake (fish of age 3) to the median of the observations at the end of year 2 (fish of age 4). Reducing P from 0.55 to 0.45 after year 1 produced a 4% reduction in the annual forage requirement under the VERY LOW survival scenario, a 16% reduction under the LOW scenario, and a 25% reduction under the MODERATE scenario.

Results

The following results are based on simulations run with the 10-18 ºC annual temperature function and cohorts with initial populations of 25,000 200-g fish, stocked annually on 15 November at age 2.

Weight of fish removed and size at harvest

The mean size at death for fish of harvestable size increased with the annual survival of harvestable fish (Table 4). This mean size varied during year, with the minimum occurring when the youngest cohort attained harvestable size. In the VERY LOW survival scenario, the monthly means varied by a factor of two; the variation diminished with higher survival.

As simulated, 5 metric tons of brown trout were stocked annually. The weight of fish removed from the population before reaching harvestable size was 6.6-7.1 metric tons annually, depending on the survival scenario. The weight of harvestable fish removed, whether by harvest or natural causes, was 1.6-18.1 metric tons annually, depending on the survival scenario.

Forage requirements

Simulated seasonal and annual forage requirements for the brown trout population are summarized in Table 5 (biomass of forage fish) and Table 6 (number of forage fish). We divided the year into three four-month seasons: winter (mid-November to mid-March); spring-early summer (mid-March to mid-July); and later summer-fall (mid-July to mid-November). These seasonal

Table 4. Simulated expected mortality, mean weight at death, and annual weight removed from the brown trout population. S_1 is survival from stocking to harvestable size (15 in); S_2 is annual survival of harvestable fish (≥15 in).

	Survival		***Expected annual mortality***		***Mean weight at death (kg)***		***Annual weight removed (metric tons)***	
Survival scenario	S_1	S_2	***Fish <15 in***	***Fish ≥ 15 in***	***Fish <15***	***Fish ≥ 15 in***	***Fish <15 in***	***Fish ≥ 15 in***
1 VERY LOW	5%	10%	23,750	1,250	0.30	1.29	7.13	1.6
2	5%	30%	23,750	1,250	0.30	2.03	7.13	2.4
3	5%	50%	23,750	1,250	0.30	2.94	7.13	3.5
4	15%	10%	21,250	3,750	0.33	1.28	7.10	4.7
5 LOW	15%	30%	21,250	3,750	0.33	1.97	7.10	7.2
6	15%	50%	21,250	3,750	0.33	2.91	7.10	10.6
7	25%	10%	18,750	6,250	0.35	1.27	6.57	7.9
8	25%	30%	18,750	6,250	0.35	1.97	6.57	12.2
9 MODERATE	25%	50%	18,750	6,250	0.35	2.92	6.57	18.1

Table 5. Simulated seasonal and annual biomass of forage required by the brown trout population. S_1 is survival from stocking to harvestable size (15 in); S_2 is annual survival of harvestable fish (≥15 in). Winter spans mid-November to mid-March; spring, mid-March to mid-July; late summer-fall, mid-July to mid-November. All cohorts were initiated with fish of age 2 on 15 November.

Survival scenario	***Survival***		***Winter (metric tons)***			***Spring-early summer (metric tons)***			***Late summer-fall (metric tons)***			***Entire year (metric tons)***		
	S_1	***S_2***	***Age class 2***	***Age classes 3-11***	***All***	***Age class 2***	***Age classes 3-11***	***All***	***Age class 2***	***Age classes 3-11***	***All***	***Age class 2***	***Age classes 3-11***	***All***
1 VERY LOW	5%	10%	9.5	1.1	10.6	2.5	0.7	3.2	1.4	0.4	1.9	13.5	2.2	15.7
2	5%	30%	9.5	3.7	13.2	2.7	3.4	6.1	2.1	2.7	4.8	14.3	9.8	24.1
3	5%	50%	9.5	8.5	18.1	2.8	8.9	11.7	2.6	7.7	10.3	14.9	25.2	40.1
4	15%	10%	13.1	3.0	16.2	7.1	2.1	9.2	4.4	1.1	5.5	24.7	6.2	30.9
5 LOW	15%	30%	13.1	10.0	23.1	7.7	9.3	17.0	6.7	7.0	13.7	27.5	26.2	53.7
6	15%	50%	13.1	25.0	38.1	7.9	26.1	34.0	8.1	22.6	30.7	29.1	73.7	102.8
7	25%	10%	15.5	4.9	20.4	11.8	3.3	15.1	7.5	1.7	9.2	34.8	10.0	44.7
8	25%	30%	15.5	17.0	32.5	12.7	15.9	28.6	11.3	11.8	23.2	39.5	44.8	84.2
9 MODERATE	25%	50%	15.5	43.4	58.9	13.2	45.5	58.7	13.9	39.6	53.5	42.5	128.5	171.0

Table 6. Simulated seasonal and annual numbers of forage fish required by the brown trout population. S_1 is survival from stocking to harvestable size (15 in); S_2 is annual survival of harvestable fish (≥15 in). Winter spans mid-November to mid-March; spring, mid-March to mid-July; late summer-fall, mid-July to mid-November. All cohorts were initiated with fish of age 2 on 15 November.

	Survival		***Winter (millions)***			***Spring-early summer (millions)***			***Late summer-fall (millions)***			***Entire year (millions)***		
Survival scenario	S_1	S_2	***Age class 2***	***Age classes 3-11***	***All***	***Age class 2***	***Age classes 3-11***	***All***	***Age class 2***	***Age classes 3-11***	***All***	***Age class 2***	***Age classes 3-11***	***All***
1 VERY LOW	5%	10%	1.7	0.2	1.9	0.6	0.2	0.7	0.4	0.1	0.6	2.7	0.5	3.2
2	5%	30%	1.7	0.7	2.4	0.6	0.8	1.4	0.6	0.8	1.5	2.9	2.3	5.2
3	5%	50%	1.7	1.5	3.2	0.6	2.1	2.7	0.8	2.3	3.1	3.1	5.9	9.0
4	15%	10%	2.3	0.5	2.9	1.6	0.5	2.1	1.4	0.3	1.7	5.3	1.3	6.7
5 LOW	15%	30%	2.3	1.8	4.1	1.8	2.1	3.9	2.0	2.1	4.1	6.1	6.0	12.2
6	15%	50%	2.3	4.5	6.8	1.8	6.1	7.9	2.4	6.8	9.2	6.6	17.4	23.9
7	25%	10%	2.8	0.9	3.6	2.7	0.7	3.4	2.3	0.5	2.9	7.8	2.2	9.9
8	25%	30%	2.8	3.0	5.8	2.9	3.7	6.6	3.4	3.6	7.0	9.1	10.3	19.4
9 MODERATE	25%	50%	2.8	7.8	10.5	3.1	10.6	13.7	4.1	11.9	16.0	10.0	30.2	40.2

boundaries coincide with the times of brown trout stocking (November), forage fish assessments in Lake Jocassee (November and March), and forage fish assessment in Lake Norman (July and November or December). Forage requirements are also summarized for age class 2 (the most recently stocked fish) and age classes 3-11.

Converting the simulated prey requirements from biomass to numbers of prey required assumptions about initial prey size and growth during the season. For winter, we used the 2000-2005 median of the average size (5.6 g) in Lake Jocassee and assumed that growth during the season was negligible. This assumption seems plausible, given the temperatures and low productivity of the lake. For spring-early summer, size distributions of the forage fishes are likely to change substantially, decreasing as recruitment begins in late spring. Assuming that growth from July to November in Lake Jocassee was proportional to growth in Lake Norman, we set the average size in July at 1.87 g or one-third the average size in November. We assumed that recruitment began in mid-May and average weight decreased linearly from 5.6 g on 15 May to 1.87 g on 15 July. Finally, we assumed that the average weight increased linearly from 1.87 g on 15 July to 5.6 g on 15 November. The daily biomass of prey was divided by the average weight of forage fish on that day to estimate the number of forage fish required. These computations assume that predation by the brown trout is not size-selective. If the brown trout consume prey larger or smaller than the average size, the number of prey consumed changes inversely.

The annual forage requirement for the brown trout population depended strongly on survival (Tables 5 and 6, Figure 13), varying by an order of magnitude (16 to 171 metric tons or 3.2 to 40.2 million fish) over the range of values tested. In the VERY LOW survival scenario, age class 2 dominated the forage requirement, and the heaviest demand occurred immediately after stocking

(Tables 5 and 6, Figure 14). With increasing survival, the older age classes made greater contributions.

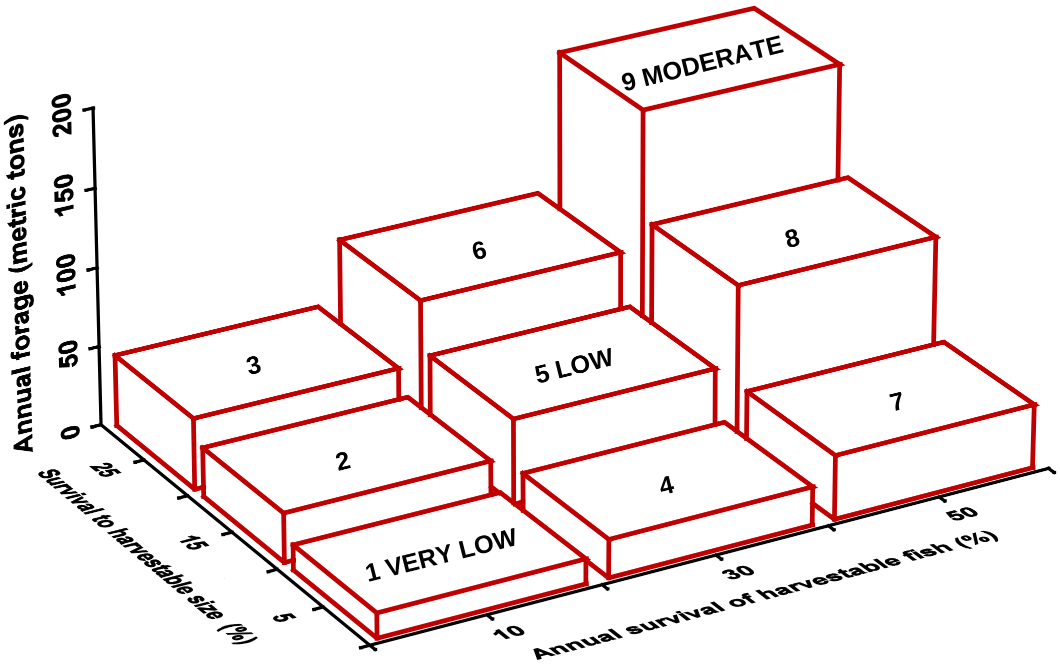

Figure 13. Simulated annual forage requirement. Blocks are labeled with scenario numbers. Data are presented in Table 5.

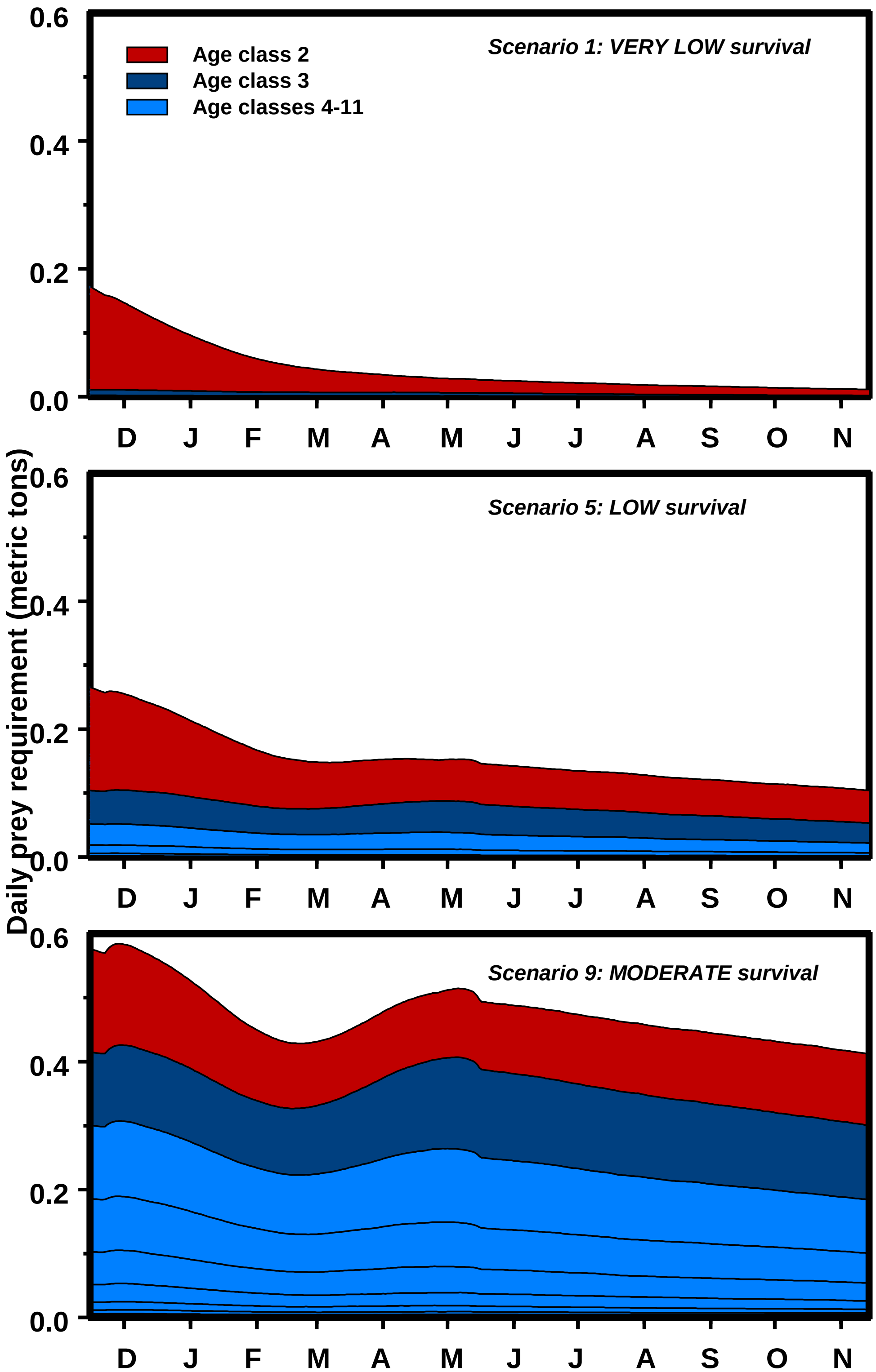

Figure 14. Simulated daily forage requirement. All cohorts were initiated with fish of age 2 on 15 November.

The simulated forage requirement is sensitive to the shape of the survival curve, particularly for age class 2. In Scenario 1, if most of the mortality occurred shortly after the cohort was stocked, rather than at a constant per capita rate, the winter forage requirement for the population could decrease by as much as 75%. If most of the mortality occurred shortly before the cohort attained harvestable size, the winter forage requirement for the population could increase by as much as 250%.

Comparison of forage requirements with forage populations in Lake Jocassee

We compared simulated forage requirements of brown trout with forage populations in Lake Jocassee on a seasonal basis. During winter, recruitment of forage fish is negligible. We used fall data from the annual hydroacoustic surveys (1989-2005, see Figure 9) to estimate the resource potentially available to brown trout for the entire season. Because threadfin shad and blueback herring spawn in late spring and early summer, we used spring data from hydroacoustic surveys to estimate the amount forage available during the spring only (mid-March to mid-May). We recomputed the forage requirement accordingly. There are few data on forage fish populations in Lake Jocasee in summer. Based on the abundance patterns for Lake Norman, we assumed that mid-July populations were four times greater than fall populations. Assuming further that recruitment after mid-July was negligible, we used these values to estimate the resource for brown trout during late summer-fall.

For Scenario 1 (VERY LOW survival), which we believe most closely describes the population in Lake Jocassee, the simulated forage requirement during winter was typically about half of the forage available in Lake Jocassee (Table 7, Figure 15). It exceeded the available forage in two of the 17 years. During spring, before recruitment to the forage population has begun, the simulated forage requirement was typically about a third of the forage available, but exceeded the available forage in

Table 7. Simulated forage requirements of brown trout for Scenario 1 (VERY LOW survival) during winter, spring, and late summer-fall, compared with forage fish populations in Lake Jocassee, 1989-2005. Percentages exceeding 100% are marked in red boldface. Note that spring spans two months only; early summer is not included.

	Simulated requirement compared with forage population (1989-2005)	
Season	***Percentage (median, range)***	***N of years >100%***
Winter (mid-November to mid-March)	48% (14%-**157%**)	2 of 17
Spring (mid-March to mid-May)	33% (8%-**4830%)**	4 of 16
Late summer-fall (mid-July to mid-November)	4% (1%-12%)	0 of 17

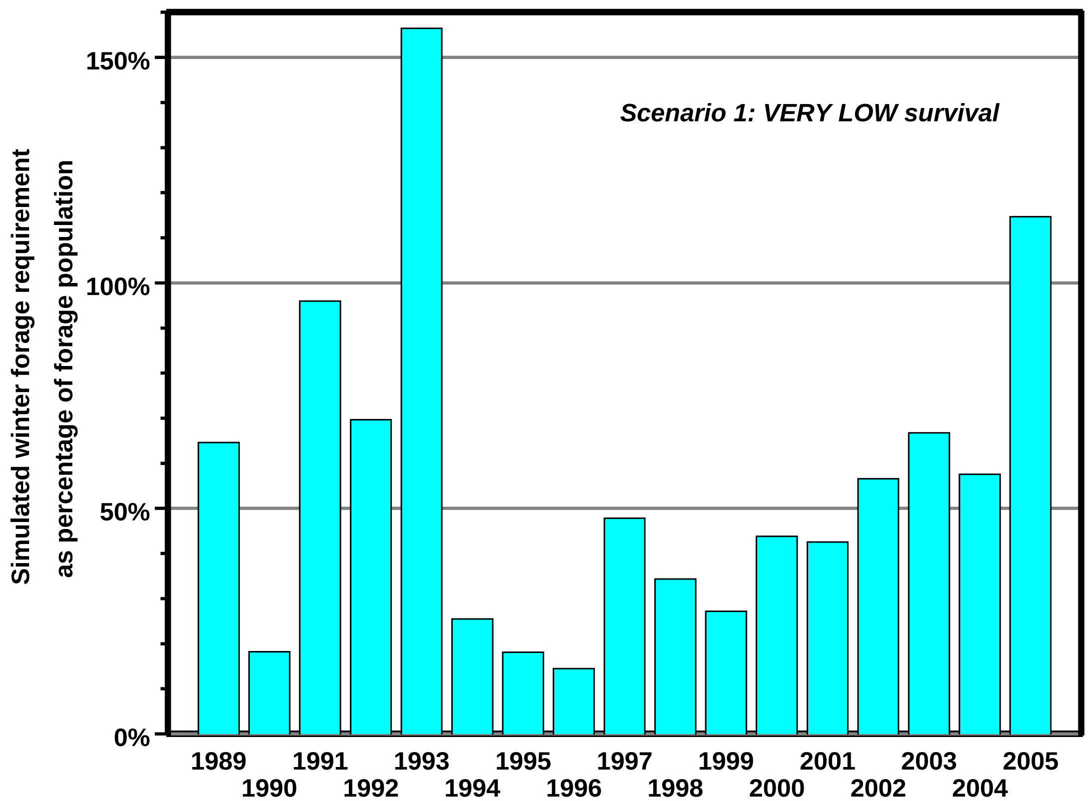

Figure 15. Simulated winter forage requirement as percentage of forage population, 1989-2005.

four of the 16 years. During late summer-fall, the simulated forage requirement was typically about 4% of the forage available and was always much less (12% at maximum) than the available forage.

The other scenarios predicted greater demands on the winter forage populations (Table 8). For Scenario 5 to 9, winter forage requirements exceeded the forage populations in many or most years. In a typical year, represented by the median fall forage population, forage would be completely consumed by mid-February in Scenario 5 and by mid-December in Scenario 9, if the brown trout were able to sustain the modeled feeding rate (Figure 16). Given the potential impact of these demands on the dynamics of the forage populations, we did not extend the comparisons for Scenarios 2 to 9 to the other seasons.

The model predicts the amount of forage required to sustain the modeled feeding rate and corresponding growth, but does not account for density-dependencies of feeding rates. Under the conditions otherwise identical to those modeled in Scenarios 1-9, attainment of harvestable size was delayed by more than a year when the feeding rate parameter was reduced by about one-third (from P=0.55 to P=0.35). Attainment of harvestable size did not occur when the feeding rate parameter was reduced by one-half. A substantial reduction in forage, such as predicted in winter, would likely affect energy expenditure on foraging, as well as feeding rates, with additional consequences for growth, condition, and possibly survival.

Table 8. Simulated forage requirements of brown trout for all scenarios during winter, compared with forage fish populations in Lake Jocassee, 1989-2005. Percentages exceeding 100% are marked in red boldface. S_1 is survival from stocking to harvestable size (15 in); S_2 is annual survival of harvestable fish (≥15 in). Winter spans mid-November to mid-March.

Survival scenario	*Survival*		*Simulated requirement compared with forage population (1989-2005)*	
	S_1	*S_2*	*Percentage (median, range)*	*N of years >100% (of 17)*
1 VERY LOW	5%	10%	48% (14%-**157%**)	2
2	5%	30%	60% (18%-**195%**)	3
3	5%	50%	81% (25%-**267%**)	6
4	15%	10%	73% (22%-**238%**)	5
5 LOW	15%	30%	**104%** (31%-**340%**)	9
6	15%	50%	**172%** (52%-**563%**)	12
7	25%	10%	92% (28%-**301%**)	8
8	25%	30%	**146%** (44%-**479%**)	12
9 MODERATE	25%	50%	**266%** (80%-**869%)**	16

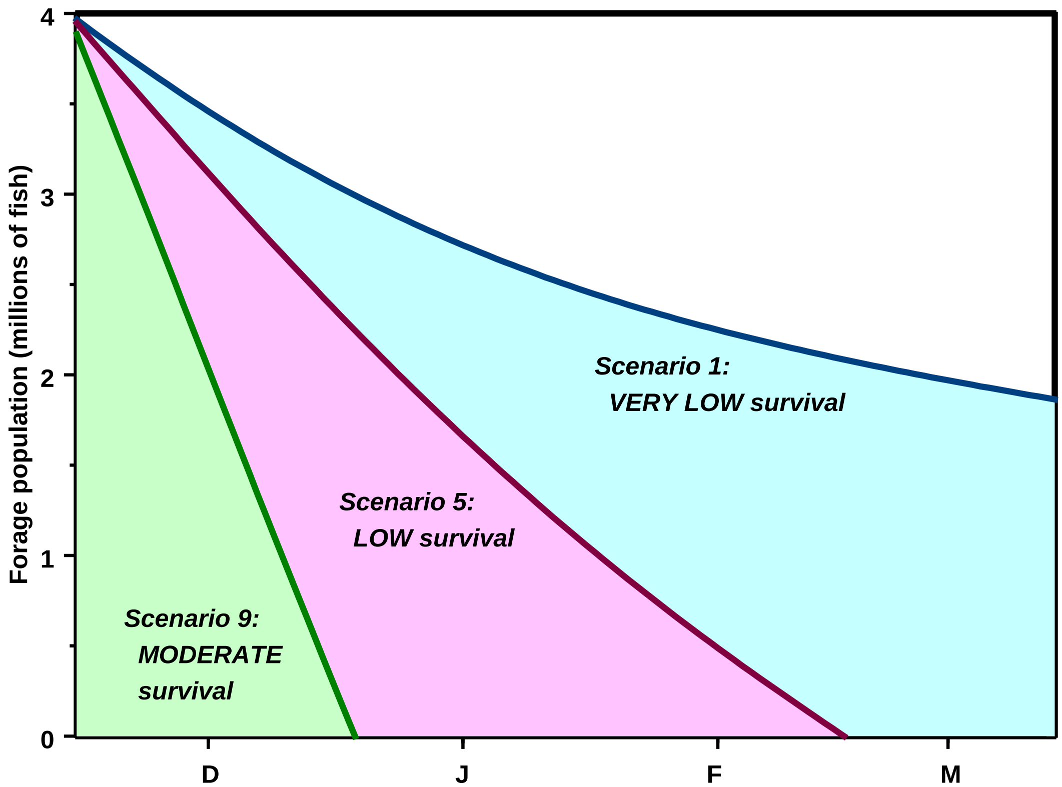

Figure 16. Impact of simulated brown trout predation on the median winter forage fish population in Lake Jocassee. Initial population of forage fish is 4 million, the median from November hydroacoustic surveys (1989-2005) in Lake Jocassee. Decline in forage fish population is due only to predation by brown trout; no other source of mortality is estimated.

Discussion

During most of the winter season (defined as mid-November to mid-March for these analyses), temperatures throughout the water column are thermally suitable (<20 °C) for brown trout (see Figure 3). The entire forage population should thus be accessible, and vulnerable, to the trout. In Scenario 1, which we believe most closely describes the population in Lake Jocassee, the winter forage requirement (1.9 million fish) is large enough to account for a substantial portion of the typical winter decline in forage fish (median decline of 2.6 million fish in 1989-2005). During winter, the brown trout in Lake Jocassee grow (see Figure 6), but relative body condition remains unchanged (see Figure 7).

Forage populations are at an annual low in spring (mid-March to mid-May for these analyses), prior to reproduction and recruitment. However, the number of forage fish, relative to simulated forage requirements for Scenario 1, was adequate in most years. The entire water column remains thermally suitable for brown trout through mid-May (see Figure 3); and nearshore aggregations of forage fish may further enhance availability of the forage fish to the trout. It is plausible that these aggregations permit the improvement in condition, and possibly faster growth, observed between March and May.

With the forage populations replenished by recruitment, conditions for the brown trout should remain favorable from mid-May through mid- to late June. By late June, the upper strata of the lake warm to temperatures above the range preferred by the trout. This constriction of habitat, which reduces access of trout to the forage fish, becomes substantial after mid-July: the upper 20-30 m of the water column is thermally unsuitable.

During late summer-fall, the supply of forage substantially exceeded the simulated requirements for Scenario 1. However, thermal stratification probably isolates the brown trout from a substantial portion of this resource. We suggest that this isolation of the trout from their forage explains the consistent deterioration of condition between May and November (see Figures 2, 7).

Thus, the field data, combined with simulation results from the VERY LOW survival scenario, give a picture of a population that experiences a short season of abundant forage in spring and, possibly, early summer. During late summer-fall, forage is abundant, but thermal stratification limits access by the trout. During the winter season, forage is initially abundant, but becomes depleted, due in part to predation by the trout. The depletion of forage may limit improvement in condition over the winter in some years, although it does not severely curtail growth. The seemingly paradoxical improvement of condition in early spring is considered above.

Substantial winter depletion of the resource is predicted under the most stringent of the survival scenarios, and the simulation results suggest that the forage base in Lake Jocassee has limited capacity to support improvements in the brown trout fishery. Increasing the annual harvest by a factor of 3 or 5 by raising survival to harvestable size (Table 4, Scenarios 4 and 7) would increase the winter forage requirement by 60 or 90% (Table 5). These requirements would exceed the forage supply in 5 years (Scenario 4) or 8 years (Scenario 7) of the 17-year record (Table 8). Alternatively, increasing the mean weight at death of harvestable fish by a factor of 1.6 to 2.3 by raising the annual survival of harvestable fish (Table 4, Scenarios 2 and 3) would increase the winter forage requirement by 30 to 70% (Table 5). These requirements would exceed the forage supply in 3 years (Scenario 4) or 6 years (Scenario 7) of the 17-year record (Table 8).

Other piscivores will further reduce the forage available in Lake Jocassee. In terms of total biomass, redeye bass is similar in abundance to brown trout in the gill net samples (130% of brown trout biomass in 2007; 60% in 2008; data from D. Rankin, SC DNR). Rainbow trout are probably not sampled so efficiently in the gill net samples (25% of brown trout biomass in 2007; 7% in 2008; data from D. Rankin, SC DNR). In the creel surveys, however, rainbow trout were similar in abundance to brown trout (93 %of brown trout biomass in 2006; 137% in 2007). Evaluation of the effects of these other species would require additional bioenergetic simulations.

Entrainment by the Bad Creek Pumped Storage Station probably has a negligible effect on the forage populations under routine conditions. Reported entrainment rates for the station are 5-18 fish/hr under routine conditions, but range up to 467 fish/hr under special conditions, such as water levels more than 4.3 m below full pool (Barwick et al., 1994). Pumping typically occurs at night and over weekends, when consumer demand for power ie lower. If we assume pumping at an average rate of 12 hr/day, the routine entrainment rates would result in removal of 7,000-26,000 forage fish during the winter season. Given that fall forage populations were 1.2-13.1 million fish (Figure 9), the impact of routine pumping should be negligible. The elevated rates observed under special conditions, if applied at 12 hr/day for the entire season, would result in removal of 120,000 forage fish during the winter season. Thus, except in years of exceptionally low fall forage populations, the impact of elevated entrainment would be small, even if the special conditions occurred throughout the season.

We caution that results from these analyses should not be interpreted to give precise predictions about the brown trout population in Lake Jocassee. Among the various uncertainties, perhaps the most important concerns survival of brown trout from stocking to harvestable size. The estimated rate was unexpectedly low. Because the youngest age class accounts for such a high proportion of the resource demand in the most realistic survival scenario, the timing of their mortality greatly affects the forage requirement.

Knowing when the stocked fish disappear is important; knowing why is even more important to broader management issues. Because the available forage seems adequate in most winters (unless the bulk of the preharvest mortality occurs late in the season), predation, illegal harvest, catch-and-release mortality of deep-caught trout, or failure to adapt to the wild are possible explanations.

If we are correct in our inferences about low survival of stocked fish, the losses must provide a substantial subsidy to some component of the system. If the fish are lost shortly after stocking, the subsidy is 4.75 metric tons, equivalent to 20-50% of the November standing stock of forage fish (see

Table 2). In Scenario 1, that quantity increases to 6.6 metric tons, equivalent to 25-70% of the November standing stock. Whether these young trout are consumed by older trout, by other piscivores, or by detritivores, their impact in the system may be substantial.

Recommendations

1) Investigate the fate of stocked brown trout during the 6-month period after stocking. Tagging fish with radiotransmitters may prove useful.
2) Obtain additional data to refine estimates of changes in growth and condition. Additional samples in April and in summer are needed.
3) If the spring stocking program resumes, use different marks for spring- and fall-stocked cohorts for at least two years; assess growth and survival.

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