Effect of Spring Discharge and Adult Abundance on Population Abundance of Two Southern Appalachian Rainbow Trout Populations

Todd D. Ewing, *Inland Fisheries Division, North Carolina Wildlife Resources Commission, 1721 Mail Service Center, Raleigh, NC 27699-17200*

James C. Borawa[1]**,** *Inland Fisheries Division, North Carolina Wildlife Resources Commission 1721 Mail Service Center, Raleigh, NC 27699-1700*

Robert P. Creed, Jr., *Department of Biology, Appalachian State University, Boone, NC 28608*

Jacob M. Rash, *Inland Fisheries Division, North Carolina Wildlife Resources Commission, 645 Fish Hatchery Road, Marion, NC 28752*

Abstract: Stream-dwelling salmonid populations may be affected by both density-dependent and density-independent processes, but the relative importance of each may vary both spatially and temporally. We quantified population fluctuations of two unexploited rainbow trout (*Oncorhynchus mykiss*) populations in western North Carolina over a 10-year period and examined the effects of spring discharge and adult abundance on recruitment. Both rainbow trout populations exhibited high degrees of temporal variability in density during the study. High spring flows that occurred during the incubation and emergence periods of rainbow trout were associated with densities of age-0 and age-1 trout in both streams. Age-0 densities were also associated with adult densities in one stream but with no evidence of a density dependent relationship. These results suggested that fluctuations in rainbow trout density in these two streams were determined primarily by a density-independent factor. Knowledge regarding the magnitude and causes of salmonid population fluctuations can allow managers to account for the high variability and statistically control for it so responses to conservation actions or perturbations are easier to detect and better inform the public about population fluctuations of a popular game fish.

Key words: year-class strength, recruitment, density-independence, discharge, *Oncorhynchus mykiss*

Journal of the Southeastern Association of Fish and Wildlife Agencies 6:67–73

Trout and salmon populations often exhibit high degrees of annual variability (Platts and Nelson 1988, House 1995). For example, in an analysis of eight published studies of five different salmonid species from 22 North American streams, Dauwalter et al. (2009) reported a mean CV of 49% for annual density of inland trout populations from streams across North America. There has been considerable debate as to the causes of these population fluctuations. Studies have suggested that density-dependent regulation resulting from intraspecific competition could be driving fluctuations in many salmonid populations (reviewed by Milner et al. 2003). However, other studies have shown that density-independent factors may be more important than density-independent factors in determining recruitment in salmonid populations (e.g., Lobón-Cerviá and Rincon 2004). There has been debate in the scientific literature as to whether density-dependent factors have a role at all in some salmonid populations (Lobón-Cerviá and Rincon 2004, Einum 2005, Lobón-Cerviá 2006). Factors regulating salmonid populations are likely context specific: in more stable systems density-dependent factors may be more important, but in unstable systems or those with peripheral habitats density-independent factors may be more important (Daufresne and Renault 2006). Because factors driving population fluctuations can differ across streams, biologists managing fluvial trout populations must understand the factors that drive these population fluctuations.

Rainbow trout (*Oncorhynchus mykiss*) are native to the western United States but were introduced into the southern Appalachian region of the eastern United States in the early 1900s and have established breeding populations throughout the region (Etnier and Starnes 1993, Jenkins and Burkhead 1993). Rainbow trout have become an important part of a very popular and economically valuable mountain trout fishery worth an estimated US$383.3 million to North Carolina's economy (Responsive Management and Southwick Associates 2015). Because of this popularity with anglers, it is important for fisheries managers to understand what factors drive population fluctuations. Here we present the analysis of two 10-year data sets for two rainbow trout populations occupying adjacent

1. Retired

tributaries of the Swannanoa River in the southern Appalachian Mountains of North Carolina. The objectives of this paper were two-fold, to 1) characterize the magnitude of fluctuations in rainbow trout populations, and 2) elucidate the factors that contribute to these fluctuations. We hypothesized that if density independent processes were important drivers of population fluctuations then there should be a strong correlation between measures of discharge and trout abundance, particularly the abundance of younger trout. Likewise, we hypothesized that if density dependent were important, then there should be evidence of a stock-recruitment curve.

Study Area

Beetree Creek and North Fork Swannanoa River are tributaries of the Swannanoa River located in the Blue Ridge physiographic province in western North Carolina. Both watersheds were virtually 100% forested, served as municipal water supplies, and were posted against trespass and closed to fishing. Further, both streams were isolated from the Swannanoa River and each other by water supply reservoirs. Thus, neither rainbow trout population in these streams experienced differential fishing mortality or immigration from other streams. The fish communities of both streams consisted of naturally reproducing populations of rainbow trout, mottled sculpin (*Cottus bairdii*), blacknose dace (*Rhinichthys obtusus*), longnose dace (*R. cataractae*), and brook trout (*Salvelinus fontinalis*). The North Fork Swannanoa River had a larger watershed, greater bankfull width, and larger bankfull discharge than Beetree Creek; elevation range and stream slope were similar between the two streams (Table 1).

Table 1. Characteristics of Beetree Creek and North Fork Swannanoa River, North Carolina, at the study sites.

	Stream	
Characteristic	Beetree Creek	North Fork Swannanoa River
Drainage area (km^2)	14.14	37.6
Elevation (m)	832 to 875	860 to 915
Bankfull width (m)[a]	9.78	21.1
Bankfull discharge (m^3 sec^{-1})[a]	6.57	24.2
Stream slope (%)	4.8	5.0
Strahler stream order	3	4
Dominant substrate	cobble, boulder	cobble, boulder

a. From Harman et al. (2000)

Methods

Rainbow Trout Sampling

Rainbow trout were sampled in both streams annually from 1991 to 2000 in early- to mid-October. In each stream, three stream segments of approximately 100 m each were sampled, chosen to ensure that at least two pool/riffle sequences were included in each segment. The same segments were sampled and site dimensions measured for each stream each year of the study. Sample sites were isolated with block nets to prevent fish movement into or out of the study area. Fish were then collected using three-pass depletion in an upstream direction. One Coffelt backpack electrofishing unit (Coffelt Manufacturing, Inc., Flagstaff, Arizona) was used for each 3 m of mean stream wetted width. All rainbow trout were measured (TL, mm) and then released.

All rainbow trout were then placed into age categories using the length-frequency method (Quist et al. 2012). Age-0 and age-1 rainbow trout were readily grouped into age categories. However, age-2 and older were difficult to distinguish so they were pooled and designated as age-2+. Though exact length categories varied slightly across years, age-0 fish were typically 40–95 mm TL, age-1 fish were usually 100–150 mm TL, and age-2+ fish were generally >150 mm TL.

Data Analyses

In each study stream, separate population estimates were made for each age class as well as all age classes combined with a maximum-likelihood procedure (Van Deventer and Platts 1983) using the computer program Microfish ver. 3.0 (Van Deventer and Platts 1989). Using the population estimates and sample area, fish density (number ha^{-1}) was calculated for each stream segment and the average of the three stream segments was calculated for each year to facilitate subsequent statistical analyses. As with the population estimates, densities were calculated for each age class, and all age classes combined.

The magnitudes of annual fluctuations in population density were calculated using the CV, which has been found to be a suitable measure for variations in population density because it is usually independent of the mean (McArdle et al. 1990). Calculating CV allowed for comparisons with the salmonid populations summarized in Dauwalter et al. (2009). A CV was calculated for the age-0, age-1, and age-2+ classes and the total rainbow trout density from each stream. Differences in CV for each age class from the two streams were tested using Feltz and Miller's (1996) asymptotic test.

To evaluate how discharge during the early stages of the rainbow trout life cycle affected recruitment, we determined the maximum instantaneous discharge that occurred from 1 March through 31 May of each year (Spring Qmax). This time frame covers both the incubation period (beginning late February to early March; Lennon and Parker 1960, Neves and Brayton 1982) and the peak emergence period (late April to late May; Fausch et al. 2001) of southern Appalachian rainbow trout. We obtained instantaneous discharge data from U.S. Geological Survey gaging station numbers 03450000 (Beetree Creek) and 3448944205 (North Fork Swannanoa River) located immediately downstream of the study sites in each stream. Simple linear regression was used to relate the annual density of age-0 fish and Spring Qmax from the same year, and age-1 rainbow trout density from a given year with Spring Qmax from the previous year. Instantaneous discharge data were not available for North Fork Swannanoa River in 1990, so only nine years of flow data were used for that stream to calculate discharge versus age-1 density. Simple linear regression was also used to test whether Spring Qmax had any effects on age-1 or age-2 fish within the same year.

To measure any potential density-dependent effects, we attempted to determine what, if any type of stock-recruitment relationship existed between the age-2+ fish and the age-0 fish. We tested for a linear stock-recruit relationship using simple linear regression to compare recruitment (age 0) to spawning stock (age 2+). We tested for the presence of a Beverton-Holt stock-recruit relationship using nonlinear regression to evaluate the formula $R = 1/(a+b/S)$ where R = age-0 fish, S = age-2+ fish, and a and b are coefficients fitted by the model (Prager et al. 1989).

We also constructed models to evaluate the combined effects of discharge and spawning stock on recruitment. A linear relationship was tested using multiple linear regression using age-0 fish as the dependent variable and age-2+ fish and Spring Qmax as the independent variables. To evaluate the effects of a nonlinear stock-recruit relationship along with Spring Qmax, we used nonlinear regression to evaluate the formula $R = 1/(a+b/S) * e^{(cQ)}$, where R = age-0 fish, S = age-2+ fish, Q = Spring Qmax, and a, b, and c are coefficients fitted by the model (modified from Maceina and Pereira 2007). Statistical significance of all nonlinear regression models was determined by using simple linear regression to compare predicted vs. actual age-0 density (Maceina and Pereira 2007), and all regression models were compared using the corrected Akaike's Information Criterion (AICc; Brown and Guy 2007). Discharge and density data were $\log_{10}$ transformed prior to all regression analyses.

Linear and nonlinear regressions were conducted using Statistix version 10 (Analytical Software, Tallahassee, Florida). All other statistical analyses were made using the R programming language (R Core Team 2017). Additionally, comparisons of coefficients of variation utilized the R package cvequality (Marwick and Krishnamoorthy 2016). A $P < 0.05$ was used to determine statistical significance for all tests.

Results

Density of total rainbow trout ranged from 897 to 3663 fish ha^{-1} for Beetree Creek and 958 to 2201 fish ha^{-1} for North Fork Swannanoa River. Density of age-0 rainbow trout ranged from 317 to 2227 fish ha^{-1} for Beetree Creek and 290 to 899 fish $ha^{-1}$for North Fork Swannanoa River. Density of age-1 rainbow trout ranged from 144 to 1035 fish ha^{-1} for Beetree Creek and from 415 to 1095 fish ha^{-1} for North Fork Swannanoa River. Density of age-2+ rainbow trout ranged from 168 to 401 fish ha^{-1} for Beetree Creek and from 187 to 555 fish ha^{-1} for North Fork Swannanoa River (Table 2). Population fluctuations, as measured by CV, ranged from 41% for all rainbow trout in Beetree Creek to 23% for North Fork Swannanoa River (Table 2), and were similar between streams for each age class (*D'AD* range 0.14 to 1.66; $P \geq 0.17$). Also, variation of age-0 fish was similar to that of age-1 and age-2+ fish in both streams during this study (*D'AD* range 0.003 to 1.380; $P \geq 0.24$). Likewise, CV of age-1 rainbow trout density was similar to that of age-2+ fish in both streams (*D'AD* range 0.26 to 1.27; $P \geq 0.26$).

Table 2. Mean annual trout density (SE; rainbow trout per ha), overall mean density, and coefficient of variation (CV) for each age class and all age classes combined for Beetree Creek and North Fork Swannanoa River, North Carolina.

	Beetree Creek				North Fork Swannanoa River			
Year	Age 0	Age 1	Age 2+	All	Age 0	Age 1	Age 2+	All
1991	484 (243)	400 (79)	378 (78)	1263 (383)	604 (139)	734 (159)	555 (163)	1893 (229)
1992	929 (268)	246 (66)	240 (59)	1415 (185)	385 (125)	789 (60)	358 (98)	1532 (59)
1993	583 (279)	680 (56)	183 (23)	1446 (234)	439 (15)	965 (94)	318 (76)	1722 (181)
1994	317 (176)	299 (7)	281 (91)	897 (271)	290 (104)	481 (68)	187 (42)	958 (22)
1995	1340 (508)	144 (43)	187 (16)	1671 (542)	562 (57)	415 (30)	328 (84)	1305 (136)
1996	1706 (63)	687 (60)	201 (12)	2594 (57)	899 (90)	638 (96)	325 (46)	1863 (90)
1997	2227 (496)	1035 (46)	401 (101)	3663 (418)	661 (112)	1095 (105)	465 (134)	2221 (122)
1998	1237 (158)	869 (39)	237 (19)	2343 (125)	380 (70)	989 (153)	226 (69)	1596 (148)
1999	1357 (133)	583 (159)	168 (41)	2107 (284)	294 (42)	593 (158)	233 (41)	1120 (235)
2000	1089 (248)	708 (34)	218 (10)	2015 (231)	551 (219)	573 (162)	291 (62)	1415 (165)
Mean	1127	565	249	1941	507	727	329	1563
CV	0.52	0.51	0.33	0.41	0.37	0.31	0.34	0.24

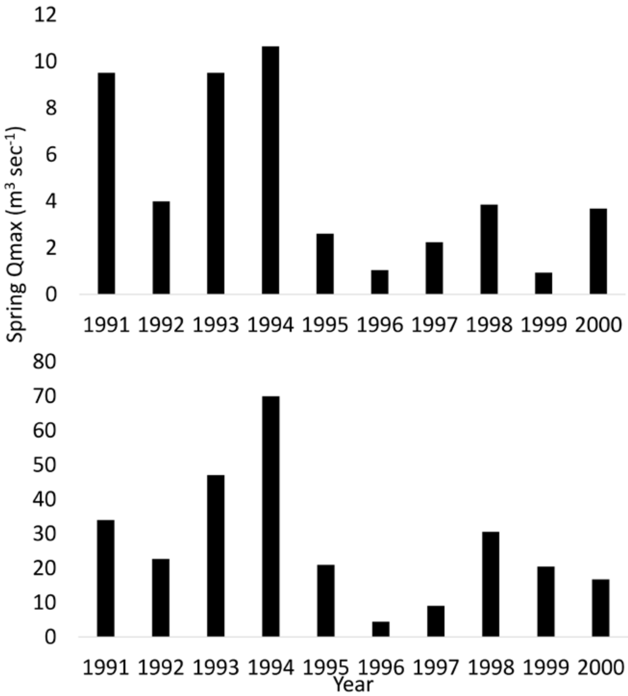

Figure 1. Spring Qmax values for Beetree Creek (top panel) and North Fork Swannanoa River (bottom panel) for the period 1991–2000.

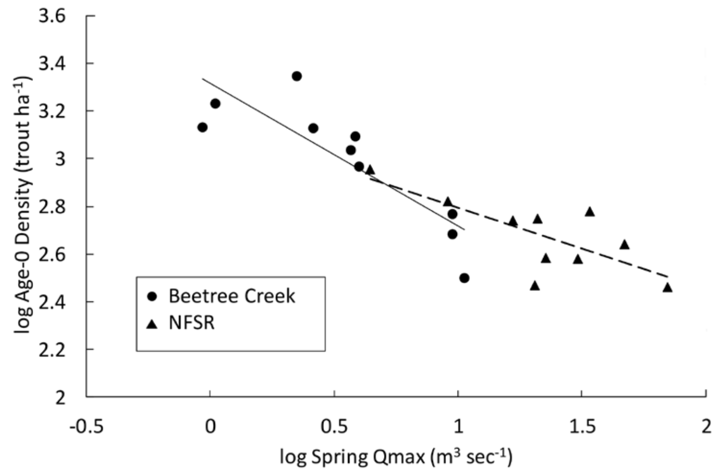

Figure 2. Relationship between age-0 rainbow trout density and the maximum instantaneous spring discharge (Spring Qmax) in Beetree Creek ($r^2=0.73$; $P=0.002$) and North Fork Swannanoa River ($r^2=0.55$; $P=0.014$). Solid line is the best fit line for Beetree Creek and the dashed line is the best fit line for North Fork Swannanoa River. NFSR = North Fork Swannanoa River.

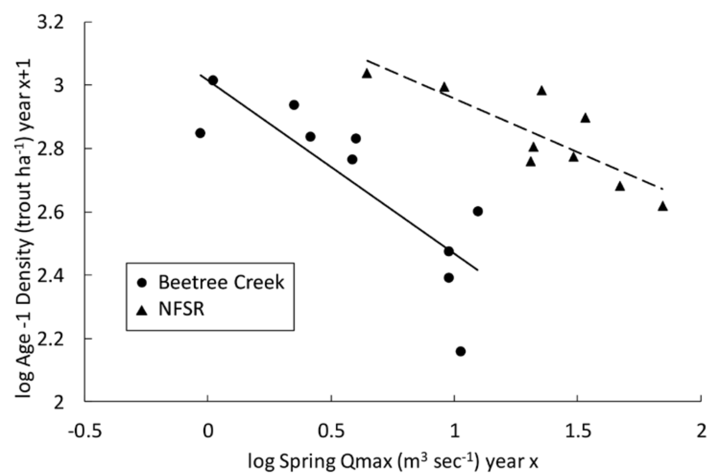

Figure 3. Relationship between age-1 rainbow trout density and the maximum instantaneous spring discharge (Spring Qmax) in the prior year in Beetree Creek ($r^2=0.69$; $P=0.003$) and North Fork Swannanoa River ($r^2=0.69$; $P=0.006$). Solid line is the best fit line for Beetree Creek and the dashed line is the best fit line for North Fork Swannanoa River. NFSR = North Fork Swannanoa River.

Spring Qmax was variable for the study period, differing with at least an order of magnitude difference between the minimum and maximum (Figure 1). In Beetree Creek, Spring Qmax ranged from 0.93 m^3 sec^{-1} to 12.43 m^3 sec^{-1} and ranged 4.42 m^3 sec^{-1} to 69.9 m^3 sec^{-1} in North Fork Swannanoa River. There was a strong negative correlation between the density of age-0 rainbow trout collected in the fall and Spring Qmax for both Beetree Creek (Figure 2; $r=-0.85$, $P=0.002$, AICc = –30.702) and North Fork Swannanoa River (Figure 2; $r=-0.74$, $P=0.014$, AICc = –35.92). There was also a strong negative correlation between the density of age-1 rainbow trout collected in the fall and the maximum instantaneous discharge during the spring of the previous year in both streams (Figure 3; $r=-0.83$, $P=0.003$ for Beetree Creek and $r=-0.83$, $P=0.006$ for North Fork Swannanoa River). There were no significant effects of Spring Qmax on age-1 or age-2+ density within the same year for either stream ($r<0.3$, $P>0.28$ for all stream/age combinations).

There was no relationship between age-2+ fish and age-0 fish in Beetree Creek as evidenced by a linear model (Figure 4; $r=0.14$, $P=0.68$, AICc = –18.00) or a Beverton-Holt model ($r=0.02$, $P=0.68$, AICc = –18.01). Both the linear model (Figure 4; $r=0.68$, $P=0.032$, AICc = –34.01) and the Beverton-Holt model ($r=0.68$, $P=0.032$, AICc = –34.14) showed a statistically significant relationship between age-2+ fish and age-0 fish for North Fork Swannanoa River. However, the Beverton-Holt model was virtually indistinguishable from a linear relationship indicating that density-dependent factors exhibited little influence on this population.

Models that combined age-2+ fish with Spring Qmax were statistically significant for both streams (Table 3). However, for Beetree Creek, neither the linear or nonlinear models combing adult abundance with the environmental variable were better than the model using the environmental variable as evidenced by AICc scores (Table 3). For North Fork Swannanoa River, the nonlinear

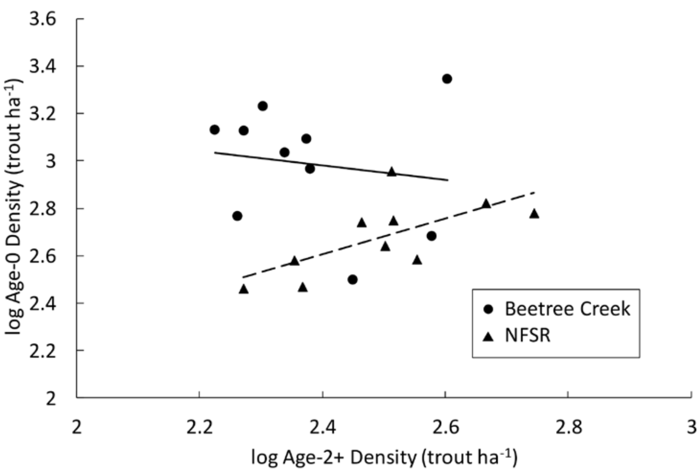

Figure 4. Relationship between age-0 and age-2+ rainbow trout density in Beetree Creek ($r^2 = 0.02$; $P = 0.68$) and Fork Swannanoa River ($r^2 = 0.46$; $P = 0.03$). Solid line is the best fit line for Beetree Creek and the dashed line is the Beverton-Holt fit for North Fork Swannanoa River. NFSR = North Fork Swannanoa River.

Table 3. Comparison of models tested to determine the effects of age-2+ (stock) density and Spring Qmax on age-0 (recruit) density for Beetree Creek and North Fork Swannanoa River. R = age-0 fish, S = age-2+ fish, Q = Spring Qmax, and a, b, and c are coefficients fitted by the model. BT = Beetree Creek, NFSR = North Fork Swannanoa River.

Model	Stream	R^2	P	AICc
Linear (effects of Spring Qmax) R = aQ + b	BT	0.73	0.002	−30.702
Linear (effects of adult density) R = aS + b	BT	0.02	0.68	−18.00
Nonlinear (effects of adult density) R = 1/(a+b/S)	BT	0.02	0.68	−18.01
Linear (effects of adult density and Spring Qmax) R = aS + bQ + c	BT	0.76	0.007	−26.074
Nonlinear (effects of adult density and Spring Qmax) R = 1/(a+b/S) $*e^{(cQ)}$	BT	0.75	0.001	−25.528
Linear (effects of Spring Qmax) R = aQ + b	NFSR	0.55	0.014	−35.92
Linear (effects of adult density) R = aS + b	NFSR	0.46	0.032	−34.01
Nonlinear (effects of adult density) R = 1/(a+b/S)	NFSR	0.46	0.031	−34.14
Linear (effects of adult density and Spring Qmax) R = aS + bQ + c	NFSR	0.75	0.008	−35.806
Nonlinear (effects of adult density and Spring Qmax) R = 1/(a+b/S) $*e^{(cQ)}$	NFSR	0.76	0.001	−36.083

model, which combined a Beverton-Holt model with the effects of Spring Qmax had the most explanatory power (Table 3).

Discussion

The large annual fluctuations in density exhibited by rainbow trout in Beetree Creek and North Fork Swannanoa River were similar to those reported for rainbow trout populations (CVs of 25%–108%) from various locations across North America (Dauwalter et al. 2009). However, these were lower than those reported from streams in the native range of rainbow trout (Platts and Nelson 1988). Highly variable population sizes are typical of trout populations in smaller streams, but it appears that those found in our study were generally comparable to those reported by other researchers.

Variations in year-class strength in our two study streams appeared to be driven by mainly by environmental fluctuations in the form of peak discharge during the incubation and emergence phases of the life cycle. As Spring Qmax increased, the age-0 density was reduced for the same year and accordingly, the age-1 rainbow trout density observed the following year was also lower. The estimates of the effects of Spring Qmax on the age-1 rainbow trout are probably more reliable than the effects shown on the age-0 class. Age-0 fish may have been under sampled, especially in North Fork Swannanoa River, because electrofishing is more effective on larger salmonids and less effective in larger streams (Bohlin et al. 1989). Spring Qmax explained 69% of the variation in density of age-1 rainbow trout the following year in both Beetree Creek and North Fork Swannanoa River. Thus, environmental factors appeared to drive the population fluctuations of rainbow trout, at least through age 1. This matches the conclusions of others for southern Appalachian rainbow trout populations (Freeman et al. 1988, Kanno et al. 2017). These results were also consistent with previous studies on multiple salmonid species across North American and Europe, indicating that salmonid population densities are typically regulated by discharge patterns during the incubation and emergence life stages (Anderson and Nehring 1985, Thorne and Ames 1987, Latterell et al. 1998, Jensen and Johnsen 1999, Spina 2001, Cattanéo et al. 2002, Lobón-Cerviá and Mortensen 2005, Unfer et al. 2011, Kanno et al. 2015, Kanno et al. 2017.

A biotic factor, age-2+ density, was also important in determining age-0 density in North Fork Swannanoa River. However, this was not the case in Beetree Creek where age-2 density had no discernable effect on age-0 density. This is consistent with the river continuum concept (Vannote et al. 1980) that suggests that biotic factors gradually become more important in larger streams. However, the relationship between age-2+ fish and age-0 fish was linear or almost so such that age-0 fish density was directly proportionate to age-2+ density. This suggested that density-dependent factors were not a significant driver of the population fluctuations observed in North Fork Swannanoa River.

We did not attempt to determine the exact mechanisms driving these fluctuations, but several studies have demonstrated that high flows can destroy salmonid redds. Corning (1969) noted that 100% of rainbow trout redds in a Colorado stream were destroyed by a high-release event from an upstream reservoir. Similarly, Kondolf et al. (1991) demonstrated that large flows can displace spawning gravels in steep Sierra Nevada streams that were otherwise stable during lower flow periods. Dechant and West (1985) noted that 7 of 15 brown trout (*Salmo trutta*) redds were either washed out or silted-in following a flood event in a southern Appalachian stream in North Carolina. Destruction of redds resulting from both scour and siltation can lead to dramatic reductions in egg viability and emergence of fry from redds (Corning 1969, Dechant and West 1985). High-flow events can also harm salmonids after emergence from redds through advection and displacement during high discharge events the first few weeks following swim-up (Irvine 1986, Heggenes and Traaen 1988). Adult fish are likely less affected by these high discharge events as evidenced by the lack of effect of Spring Qmax on age-1 or age-2+ fish abundance in the same year observed in our study.

Because our data are correlative, we cannot rule out the possibility that some other factor associated with Spring Qmax drove these population dynamics (Fausch et al. 2001). However, the high amount of variance in recruitment explained by Spring Qmax is strong evidence that this factor or a related factor is a likely cause. Ultimately, experimental studies may be needed to investigate specific factors to decipher the relative impact of various biotic and abiotic processes on trout population fluctuations.

Knowledge of the magnitude and causes of these population fluctuations will allow fishery managers to explain factors limiting rainbow trout recruitment and predict years when angling success may decline. Given the popularity and economic importance of trout fisheries, it will be extremely important to communicate this information to the fishing public. Additionally, high population variability can mask impacts of perturbations or management actions on fish populations (Platts and Nelson 1988, House 1995). For example, using the guidance of Dauwalter et al. (2009) it would require almost 20 years of data in Beetree Creek and approximately 15 years of data in North Fork Swannanoa River to detect a 5% annual decline in rainbow trout assuming an $\alpha = 0.05$ and $\beta = 0.2$. However, with knowledge of the relationship between flow and density fluctuations, it may be possible for researchers to account for the high variability and statistically control for it so trends are easier to detect. Biologists managing fluvial trout fisheries need to be aware that salmonid recruitment can vary substantially among years and consider the effects of these population fluctuations on evaluations of restoration and management activities.

Acknowledgments

The data used for this study was collected through projects funded through a Federal Aid in Sport Fish Restoration grant. The authors would like to thank the many North Carolina Wildlife Resources Commission staff that assisted with the trout sampling. We also thank Chris Goudreau, Kevin Dockendorf, Bryan Brown, Tom Kwak, Ryan Heise and T. R. Russ for helpful comments on earlier versions of this manuscript. This paper was greatly improved by the suggestions and comments of Steve Sammons and two anonymous reviewers.

Literature Cited

Anderson, R. M. and R. B. Nehring. 1985. Impacts of stream discharge on trout rearing habitat and trout recruitment in the South Platte River, Colorado. Pages 59–64 *in* F. W. Wilson, R. G. White, and R. H. Hamre, editors. Proceedings of the Symposium on Small Hydropower and Fisheries. Aurora, Colorado.

Bohlin, T., S. Harmin, T. G. Heggberget, G. Rasmussen, and S. J. Saltveit. 1989. Electrofishing-theory and practice with special emphasis on salmonids. Hydrobiologia 173:9–43.

Brown, M. L. and C. S. Guy. 2007. Science and statistics in fisheries research. Pages 1–30 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Cattanéo, F., N. Lamouroux, P. Breil, and H. Capra. 2002. The influence of hydrological and biotic processes on Brown Trout (*Salmo trutta*) population dynamics. Canadian Journal of Fisheries and Aquatic Science 59:12–22.

Corning, R. V. 1969. Water fluctuation, a detrimental influence on trout streams. Proceedings of the Southeastern Association of Game and Fish Commissioners 23:431–454.

Daufresne, M. and O. Renault. 2006. Population fluctuations, regulation and limitation in stream-living brown trout. Oikos 113:459–468.

Dauwalter, D. C., F. J. Rahel, and K. G. Gerow. 2009. Temporal variation in trout populations: implications for monitoring and trend detection. Transactions of the American Fisheries Society 138:38–51.

Dechant, T. and J. L. West. 1985. Characteristics and success of wild brown trout redds in two western North Carolina streams. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 39:86–96.

Etnier, D. A. and W. C. Starnes. 1993. The fishes of Tennessee. University of Tennessee Press, Knoxville.

Einum, S. 2005. Salmonid population dynamics: stability under weak density dependence? Oikos 110:630–633.

Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. Ecological Applications 11:1438–1455.

Feltz C. J. and G. E. Miller. 1996. An asymptotic test for the equality of coefficients of variation from k populations. Statistics in Medicine 15:647–658.

Freeman, M. C., M. K. Crawford, J. C. Barrett, D. E. Facey, M. G. Flood, J. Hill, D. J. Stouder, and G. D. Grossman. 1988. Fish assemblage stability in a southern Appalachian stream. Canadian Journal of Fisheries and Aquatic Science 45:1949–1958.

Harman, W. A., D. E. Wise, M. A. Walker, R. Morris, M. A. Cantrell, M. Clemmons, G. D. Jennings, D. Clinton, and J. Patterson. 2000. Bankfull regional curves for North Carolina mountain streams. Pages 185–190 *in* D. L. Kane, editor. Proceedings of American Water Resources Association Specialty Conference on Water Resources in Extreme Environments. Anchorage, Alaska.

Heggenes, J. and T. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. Journal of Fish Biology 32:717–727.

House, R. 1995. Temporal variation in abundance of an isolated population of cutthroat trout in western Oregon, 1981–1991. North American Journal of Fisheries Management 15:33–41.

Irvine, J. R. 1986. Effects of varying discharge on the downstream movement of salmon fry, *Oncorhynchus tshawytscha* Walbaum. Journal of Fish Biology 28: 17–27.

Jenkins, R. R. and N. M. Burkhead. 1993. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Jensen, A. J. and B. O. Johnsen. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Functional Ecology 13:778–785.

Kanno, Y., M. A. Kulp, S. E. Moore, and G. D. Grossman. 2017. Native brook trout and invasive rainbow trout respond differently to seasonal weather variation: spawning timing matters. Freshwater Biology 62:868–879.

———, K.C. Pregler, N. P. Hitt, B. H. Letcher, D. J. Hocking, and J. E. Wofford. 2015. Seasonal temperature and precipitation regulate brook trout young-of-the-year abundance and population dynamics. Freshwater Biology 61:88–99.

Kondolf, G. M., G. F. Cada, M. J. Sale, and T. Felando. 1991. Distribution and stability of potential salmonid spawning gravels in steep boulder-bed streams of the eastern Sierra Nevada. Transactions of the American Fisheries Society 120:177–186.

Latterell, J. J., K. D. Fausch, C. Gowan, and S. C. Riley. 1998. Relationship of trout recruitment to snowmelt runoff flows and adult trout abundance in six Colorado mountain streams. Rivers 6:240–250.

Lennon, R. E. and P. S. Parker. 1960. The stoneroller, *Campostoma anomalum* (Rafinesque), in Great Smokey Mountains National Park. Transactions of the American Fisheries Society 89:263–270.

Lobón-Cerviá, J. 2006. Instability of stream salmonid population under strong environmental limitations-a reply. Oikos 114:376–380.

——— and E. Mortensen. 2005. Population size in stream-living juveniles of lake-migratory brown trout *Salmo trutta* L.: the importance of stream discharge and temperature. Ecology of Freshwater Fish 14:394–401.

——— and P. A. Rincon. 2004. Environmental determinants or recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. Oikos 105:641–646.

Maceina, M. J. and D. L. Pereira. 2007. Recruitment. Pages 121–186 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Marwick, B. and K. Krishnamoorthy. 2016. Cvequality: Tests for the equality of coefficients of variation from multiple groups. R package version 0.1.1.

McArdle, B. H., K. J. Gaston, and J. H. Lawton. 1990. Variation in the size of animal populations: patterns, problems, and artifacts. Journal of Animal Ecology 59:439–454.

Milner, N. J., J. M. Elliott, J. D. Armstrong, R. Gardiner, J. S. Welton, and M. Ladle. 2003. The natural control of salmon and trout populations in streams. Fisheries Research 62:111–125.

Neves, R. J. and S. L. Brayton. 1982. Reproductive cycle and associated changes in energy content of the body tissues in rainbow trout from the South Fork Holston River, Virginia. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 36:358–368.

Platts, W. S. and R. L. Nelson. 1988. Fluctuations in trout populations and their implications for land-use evaluation. North American Journal of Fisheries Management 8:333–345.

Prager, M. H, S. B. Saila, and C. W. Recksiek. 1989. FISHPARM: a microcomputer program for parameter estimation of nonlinear models in fishery science. Old Dominion University Oceanography Technical Report 87–10.

Quist, M. C., M. A. Pegg, and D. R. Devries. 2012. Age and growth. Pages 267–731 *in* A. W. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries Techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Responsive Management and Southwick Associates. 2015. Mountain trout fishing: economic impacts on and contributions to North Carolina's economy. A report to the North Carolina Wildlife Resources Commission.

Spina, A. P. 2001. Incubation discharge and aspects of brown trout population dynamics. Transactions of the American Fisheries Society 130:322–327.

Thorne, R. E. and J. J. Ames. 1987. A note on variability of marine survival of sockeye salmon (*Oncorhynchus nerka*) and effects of flooding on spawning success. Canadian Journal of Fisheries and Aquatic Science 44:1791–1795.

Unfer, G., C. Hauer, and E. Lautsch. 2011. The influence of hydrology on the recruitment of brown trout in an Alpine river, the Ybbs River, Austria. Ecology of Freshwater Fish 20: 438–448.

Van Deventer, J. S. and W. S. Platts. 1983. Sampling and estimating fish populations from streams. Transactions of the Forty-Eighth North American Wildlife and Natural Resources Conference 48:349–354.

——— and ———. 1989. Microcomputer software System for Generating Population Statistics from Electrofishing Data—User's Guide for MicroFish 3.0. USDA Forest Service, General Technical Report INT-254.

Vannote, G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.